VOLUME LVII NUMBER 5

THE
BOTANICAL GAZETTE

MAY 1914

THE PROBABLE ORIGIN OF OENOTHERA LAMARCKIANA SER.

HUGO DE VRIES

(WITH PLATES XVII–XIX)

In a series of most interesting articles, B. M. DAVIS has recently tried to prove that mutability might be a result of previous crosses. This view was first proposed by BATESON and SAUNDERS, and applies especially to the phenomena which *Oenothera Lamarckiana* shows when seeds from the pure strain, and even from pure lines within this strain, are sown, as in the experiments I conducted in my experimental garden. DAVIS expected to be able to offer the desired proof by showing that *O. Lamarckiana* might be duplicated by crossing two other species of the same group. Up to this time, as a matter of fact, he has not succeeded in producing any form which comes sufficiently near *O. Lamarckiana* to be compared with it.[1] But if he had succeeded in doing so, evidently it would not have been a proof for his assertion, unless his hybrid should show the same degree of mutability as does *O. Lamarckiana*, since we have as yet no means of judging from the morphological characters of a given plant whether its hereditary characters are in a stable or in an unstable condition.

In starting his experiments to produce a duplication of LAMARCK'S evening primrose, DAVIS was unfortunate in the choice of the species for his combination. He chose *O. biennis* L. and a

[1] For a successful duplication of an elementary species by means of crossing, see *Oenothera biennis*×*O. cruciata* Nutt. in Gruppenweise Artbildung, p. 311.

form which he assumed to be *O. grandiflora* Aiton. It is evident that the first condition of success in such work consists in the purity and the immutability of the species which are to produce the hybrid. If they are already in a mutable condition, it is to be expected that their hybrids, or at least some of them, may combine the different lines of mutability of their parents; and at all events, the mutability of such a hybrid would be no proof that this phenomenon may be produced by means of crossing. On the other hand, if the species to be crossed, or even only one of them, were not pure, the hybrid might inherit this impurity and show phenomena which might easily be mistaken for mutations.

It so happens that *O. biennis* is in a condition of mutability analogous to that of *O. Lamarckiana*, although not developed to the same high degree. From time to time it produces dwarfs, which are distinguished from it by exactly the same two characters which differentiate the dwarfs of *O. Lamarckiana* from their mother species, namely, low stature and sensitiveness to the attacks of some species of soil bacteria.[2] Moreover, STOMPS has shown that *O. biennis* may, although very rarely, double the number of chromosomes in its sexual cells, which in *O. Lamarckiana* produces the two mutants *O. gigas* and *O. semigigas*.[3] As is now generally admitted, *O. gigas* results from the pairing of two mutated sexual cells, each of which had a double number of chromosomes. *O. semigigas*, on the other hand, is produced by the pairing of a sexual cell mutated in the same way, with a normal gamete; therefore it possesses only 21 chromosomes (14+7), while the number in *O. gigas* is 28. As yet, only *semigigas* mutants have been observed coming from *O. biennis*, and it is obvious that the double combination must be much rarer. As a proof of this special kind of mutability in *O. biennis*, however, the observations of STOMPS are wholly sufficient.

In quoting these facts, DAVIS says that if it can be shown "that tested strains of this *biennis* are able to produce new forms of specific

[2] STOMPS, TH. J., Mutation von *Oenothera biennis* L. Biol. Centralbl. **32**:521–535. 1912; also ZEYLSTRA, H. H., *Oenothera nanella* De Vries, eine krankhafte Pflanzenart. Biol. Centralbl. **31**:129–138. 1911. Vergl. ferner: Gruppenweise Artbildung 1913:296–304.

[3] STOMPS, TH. J., *op. cit.* p. 533.

rank or even marked varieties, the mutationists would have much stronger evidence in support of the mutation theory than that based on the behavior of *O. Lamarckiana*."[4] After conceding this strong position to his adversaries, DAVIS subjects the results of STOMPS to a rather sharp criticism, which, unfortunately, is based upon a confusion of two wholly distinct types, namely, *O. biennis* L. var. *cruciata*[5] and *O. cruciata* Nutt. He says: "It should be made clear that the form (*O. biennis cruciata*) is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters," and "a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product as a hybrid in which marked modifications of germinal constitution are to be expected."[6] But, as a matter of fact, the Dutch *O. biennis cruciata* differs from *O. biennis* only in the characters of the petals; in all other respects it is wholly the same, and therefore evidently only a subordinate variety of this species. It has not been dealt with in recent taxonomic treatments, since it occurs almost exclusively in the sand dunes of Holland, where it is produced from time to time by mutation from the mother form (first observed in 1900), without having been able until recently to multiply in the field so as to produce a persistent local variety.[7]

On the other hand, *O. cruciata* Nutt. is quite a different species, with narrow, brownish green leaves, and a different type of branching, of spikes, and of fruits. It grows wild in New York and Vermont, and is well known to all students of the American flora. By some authors it has been considered a variety of *O. biennis*, and this probably is the chief cause of DAVIS' confusion. The character and the behavior of its hybrids with *O. biennis* have been amply dealt with in my *Gruppenweise Artbildung*.

In the experiment of STOMPS, the dwarf and *semigigas* mutations were produced by hybrid strains of *O. biennis* and *O. biennis*

[4] DAVIS, B. M., Mutations in *Oenothera biennis* L.? Amer. Nat. **47**:116–121 (especially p. 116). 1913; see also *op. cit.* **47**:540–596 (especially p. 567). 1913.

[5] Die Mutations-Theorie **2**:599. 1903.

[6] Amer. Nat. **47**:117. 1913.

[7] Die Mutations-Theorie 2:599. 1903.

cruciata, and it was assumed that such strains would behave as true species in all characters not related to the differentiating marks of the petals. It must be conceded, therefore, that the cross of these two forms may be treated "as though it were the combination of forms within the same species, which have similar germinal constitutions" (DAVIS, *op. cit.* p. 117).

But the most clear and simple way of obviating this whole objection is evidently to sow seeds of *O. biennis* of pure descent upon the same large scale as in the former experiment. This has been done, and a dwarf and a *semigigas* form have been produced by this pure line, besides some other mutations.[8] They had the same characters as the former ones, and now provide us with the "strong support" asked for by DAVIS. Moreover, they show that his choice of *O. biennis* for a proof of the assertion that mutability might be produced by crossing immutable species was a most unhappy one.

The second condition for success in this kind of work is, as has been stated, the purity of the types to be crossed. As already quoted, DAVIS assumes that a cross between two very distinct evolutionary lines may give a hybrid with marked modifications of germinal constitution. This may be applied to his choice of the type which he calls *O. grandiflora*, and which he has made the other parent of his initial cross. He got his seeds from Dixie Landing, Alabama, a locality where BARTRAM had discovered *O. grandiflora* about a century ago. He assumed them to be of the pure species, but a culture which I made in my garden from seeds kindly supplied to me by Mr. DAVIS proved to be a mixture, and thereby threw a distinct doubt upon the purity of the station. For this reason I visited Dixie Landing in September 1912, and had the good fortune to be accompanied by Mr. H. H. BARTLETT, of Washington, well known for his systematic researches among the wild species of this group. We found the station in a most desolate condition. A small-flowered species, *O. Tracyi*, in almost all respects different from *O. grandiflora*, had migrated into the same old cotton fields and mixed everywhere with the species of BAR-

[8] STOMPS, TH. J., Parallele Mutationen bei den Oenotheren. Ber. Deutsch. Bot. Gesells. **30**:Heft 3, 1914.

TRAM.[9] On no single field was the original form pure; it was always mixed to such a degree with *O. Tracyi* and with their hybrids that we found it impossible to collect undoubtedly pure *grandiflora* seed from this locality. Moreover, the intermediate types were so numerous (over a dozen) that it was difficult to regard all of them as normal hybrids between only two parents. To produce such a diversity of forms, either one or both of the parents must have been in a mutating condition, or more than two species must have combined in the crosses. In both cases, the material can hardly be considered as a fit starting-point for experiments bearing upon the causal relations of crossing and mutability.

Recently I have shown that besides *O. biennis* some other species of *Oenothera* are actually in a state of mutability, and especially has one of the most common American types thrown off marked mutants in my experiment garden.[10] The degrees of development of this condition, however, are very different in different species. In some of them mutations occur rarely, but they serve to throw a doubt upon the stability of those forms for which no positive results have as yet been won. In other words, we may say that almost all the nearest allies of *O. Lamarckiana* are open to the suspicion of sharing at least some degree of the mutability of this species. There is no use, therefore, in trying to produce mutability by crosses of species of the same subgenus (*Onagra*) in order to show that this phenomenon is only a result of crossing, as is asserted by DAVIS.

Moreover, I might point out that the question should be dealt with from a general standpoint and not be limited to the evening primroses. If it should be true that phenomena like those of *O. Lamarckiana* could be produced by crossing immutable species, it would, of course, be of much higher scientific value to produce them in other families or genera, or at least in the other subgenera of the evening primroses. The chance of finding immutable parents for a cross would be far greater and the proof could be given as easily and in many cases with less amount of mechanical work

[9] DE VRIES, HUGO, and BARTLETT, H. H., The evening primroses of Dixie Landing, Alabama. Science N.S. **35**:599–601. 1912.

[10] Gruppenweise Artbildung, pp. 296–312. 1913.

and space in the garden. The line of work chosen by DAVIS seems to me to be necessarily without any chance of success.

Besides his experimental work, DAVIS has made some historical researches to discover the origin of *O. Lamarckiana*.[11] Unfortunately, he has neglected to visit the Museum d'Histoire Naturelle at Paris, where the herbarium of LAMARCK is preserved, and where other valuable documents concerning the first appearance of our species are to be found. For myself I visited these collections in 1895 and reported on the results of my investigations in my *Mutation theory* (vol. I. pp. 437–444 of the English edition). In October 1913 I repeated my visit and compared the authentic specimens with the remarks made upon them by DAVIS. I regret to say that, through his ignorance of the available evidence, DAVIS has been led to conclusions which are fully contradicted by the herbarium material, both of the "Herbier de Lamarck" and of the "Herbier général" of the Museum. As we shall see, the origin of *O. Lamarckiana* is the same as I have pointed out in my book.

In the herbarium of LAMARCK, *O. grandiflora* (Lam.), which later was renamed by SERINGE and called *O. Lamarckiana*, the name it still bears, is represented by two large flowering specimens. When I studied them in 1895, they were loose on their sheets and bore together the no. 12, indicating that they corresponded with no. 12 *O. grandiflora* of the *Encyclopédie méthodique, Botanique*, by LAMARCK.[12] About 1900 they were fastened on new sheets and the numbers have been lost.[13] For convenience, I shall call these specimens *A* and *B*, the former being represented by our pl. XVII, while a photograph of *B* has been published by DAVIS.[14]

[11] DAVIS, B. M., Was LAMARCK's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club **39**:519–533. *pls. 37–39.* 1912; A much desired *Oenothera*. Plant World **16**:145–153. 1913; The problem of the origin of *Oenothera Lamarckiana*. New. Phytol. **12**:233–241. 1913.

[12] The Mutation Theory **1**:442. 1901.

[13] The herbarium of LAMARCK was acquired by the Museum d'Histoire Naturelle in 1886. Vergl. BONNET, ED., L'herbier de LAMARCK, son histoire, ses vicissitudes, son état actuel. Jour. Botanique **16**:129–138. 1902.

[14] DAVIS, B. M., Was LAMARCK's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club **39**:519–533. 1912. See *pl. 37*.

Unfortunately, these two specimens do not belong to the same elementary species, but the question as to which of them is to be considered as the authentic specimen has been answered by all authors in the same way, with the exception of DAVIS. According to the general agreement, *A* (pl. XVII) is the type of the species. DAVIS has not seen this specimen, and has based his judgment upon the communications of botanists concerned with systematic rather than with elementary species.

The plant *A* corresponds exactly with *O. Lamarckiana* Ser. as it is now universally cultivated and as I know it from my own cultures. The specimen is evidently a side branch, picked in the autumn, and the flowers, although very large, are not quite so large as may be seen in July and August. It bears no fruits, but the sexual organs of the flowers and the form of the flower buds do not leave the least doubt concerning its identity. The stigma lobes are widely spread and raised by the long style high above the tops of the anthers, and this is one of the best characters of *O. Lamarckiana*. The buds are conical and thick, and not thin as in *O. grandiflora* Ait. For comparison, I have given a group of flower buds (pl. XVII), picked in the autumn also, from my pure cultures. All the other marks correspond to those of the present species, although of course not all of them distinguish it from allied forms.

This sheet bears the label, "d'Amérique sept., tige rameuse, haute de 3 à 4 pieds," in the handwriting of LAMARCK. The description in the *Encyclopédie* says of the origin of the species: "Cette espèce est originaire de l'Amérique septentrionale. On la cultive au jardin du Muséum d'Histoire Naturelle (V.S.)."[15] The description, however, quotes some points which are not visible on the herbarium specimen, nor on specimen *B*. It is therefore clear that the author knew his plants from another source still, probably from the living material of the Jardin des Plantes. The most interesting point for us is the description of the fruits: "Le fruit est une capsule courte, cylindrique, glabre, tronquée légèrement, quadrangulaire, n'ayant environ que le tiers de la longueur

[15] V.S. ("vidi siccum") means that the diagnosis is based on herbarium material.

du tube calicinal."[16] This description wholly agrees with the fruits of the present species, especially if we remember that LAMARCK based his description on a comparison with the only other large-flowered form he knew, *O. longiflora*. The short fruits at once distinguish our species from the allied types, such as *O. suaveolens* Desf. and *O. grandiflora* Ait., which have thin and proportionally long fruits.[17]

This character of the fruits shows that the description of the *Encyclopédie* has been based upon specimen *A* and not upon the other one. For, although *B* lacks fruits also, it belongs to an elementary species which has long and narrow fruits, as we shall soon see. Here I might point out that in systematic researches of this kind, more value is to be attached to published diagnoses and descriptions than to the material preserved in a herbarium. The older systematists, as a rule, did not take much care of their material, even if they were very careful of their descriptions.[18] The herbarium specimens are often found without their names and without any indication concerning their origin. The rule "descriptio praestat herbario" applies in our special case, even as it does in many others. In our case, the description is relatively complete and clear, while in the dried specimen only part of the characters are represented.

For all these reasons I cannot agree with DAVIS, who says (p. 519) that I made an incorrect determination of the material of my cultures, when I identified it with LAMARCK'S plant of 1796. The authentic specimen of LAMARCK and the description in the

[16] Encyclopédie méthodique, Botanique par LAMARCK, Tome IV, 1796. pp. 550–554, "Onagraire." Twelve species of this genus are enumerated, *O. longiflora* being no. 4, *O. corymbosa* no. 11, and *O. grandiflora* no. 12. A copy of the diagnosis of this last one may be found in my *Mutation theory* (p. 441) and in the article of DAVIS. The article in the *Encyclopédie* is not signed and was probably written by POIRET, who prepared many articles in vol. IV, and wrote the whole of the later volumes. In the herbarium of Paris some of the specimens may be seen quoted with the authority of POIRET, as, for example, on the sheet of *O. suaveolens* Desf., where above that name is written *Oenothera grandiflora* Poiret Encyclopédie. (Cf. *pl. 39* of the article of DAVIS.)

[17] L'*Oenothera grandiflora* de l'herbier de LAMARCK. Rev. Gén. Botanique 25: 1914.

[18] Cf. BONNETT, *op. cit.* p. 138.

Encyclopédie correspond as closely with the characters of my plants as dried specimens and descriptions expressed in words ever can do.

On the contrary, the specimen *B* is surrounded with doubts. DAVIS has given a very elaborate description of this branch, comparing it with my *Lamarckiana*. The sheet bears the label: "*Oenothera* . . . . [*grandiflora*] . . . . nova spec. flores magni lutei, odore grato, caulis 3 pedalis." The fact that the name *grandiflora* is placed in brackets shows that LAMARCK did not wholly trust his identification of this plant with the other one. Perhaps the words "nova species" indicate that he took it to be possibly a different species. Later, POIRET discovered the identity of this specimen with *O. grandiflora* Aiton Hort. Kew,[19] as has been indicated by DAVIS. And in DE CANDOLLE'S *Prodromus* (3:47. 1828), SERINGE separated the two types, describing *O. grandiflora* Ait. and *O. Lamarckiana* (SER. MSS) as different species.

The words "odore grato" point to *O. grandiflora* Ait., which has fragrant flowers, while the flowers of *O. Lamarckiana* Ser. are almost without odor. In the original description no mention is made of the odor, and this shows once more that the specimen *B* was not the authentic one for this description.

DAVIS has compared the branch *B* with some of his hybrid strains from Dixie Landing[20] and finds a close resemblance. Perhaps the plant of LAMARCK was a chance hybrid found in the Jardin des Plantes, and in this case, as DAVIS says, "we can have no certainty as to the characters of an individual plant unless its seeds have been grown in large cultures."[21] At all events, it is not backed by other herbarium material in the Museum d'Histoire Naturelle, so far as I know. If POIRET'S opinion that it belongs to *O. grandiflora* Ait. is correct, then it has evidently not served as a basis for the description of *O. grandiflora* Lam. (*O. Lamarckiana* Ser.). In *O. grandiflora* the fruits are thin and relatively large, for example,

[19] Encyclopédie méthodique. Suppl. IV, p. 141. 1816. See DAVIS, p. 522.

[20] At Dixie Landing, Alabama, only hybrid strains of *O. grandiflora* and *O. Tracyi*, perhaps mixed with other species too, are to be found. See Science *op. cit.* p. 399. 1912.

[21] DAVIS, B. M., A much desired *Oenothera*. Plant World 16:148. 1913.

3 cm. long and 3 mm. wide; while those of *O. Lamarckiana* may measure 2.5 cm. in length and 6 mm. in width, making a ratio of $\frac{10}{1}$ in the one case and $\frac{4}{1}$ in the other.[22] The description of the fruits as short, as given by LAMARCK, evidently points to the second and not to the first case.[23]

Summing up the main results of this discussion, we find that specimen *A* of the herbarium of LAMARCK closely corresponds to the *O. Lamarckiana* Ser. of the present time, and has been taken by almost all authors for its prototype. The specimen *B* differs from it in its general aspect, in the words "odore grato" on its label, and in the opinion of POIRET that it belongs to *O. grandiflora* Ait., this opinion pointing to long and narrow fruits. Personally, it impressed me as having been brought into the herbarium of LAMARCK only later on, and as having been placed in the cover of *O. grandiflora* Lam. with a doubt shown by the placing of the name in brackets.

The best proof for the fact that *A* and not *B* is the authentic specimen of *O. grandiflora* Lam. is perhaps given by the specimen in the herbarium of Father POURRET, which was given to the Muséum d'Histoire Naturelle by Dr. BARBIER in 1847.[24] It bears the name *Oenothera grandiflora* Lam. written in the clear and beautiful handwriting of the clerk of POURRET. In the same cover there is another sheet of POURRET'S collection, on which the same clerk wrote *Oenothera biennis*. Unfortunately, DAVIS, who did not visit the Museum, has mistaken this one for the one studied by me,[25] and has accordingly published a photograph (*pl. 38*) and a description of it. It is easily seen that this specimen really comes nearer to our present *O. biennis* L. than to anything else.

[22] L'*Oenothera grandiflora* de l'herbier de LAMARCK, *op. cit. fig. 1, b* and *c*.

[23] DAVIS (*op. cit.* p. 523) lays great stress on the tips of the sepals, but I cannot find a well defined difference between the two species in this character. He calls attention to the word "sétacé" in LAMARCK'S description of the sepal tips: "this has been translated by DE VRIES (*Mutations-Theorie*, p. 317. 1901) as "dicke." The French, however, is from the late Latin word *setaceus*, derived from "seta," a stiff hair or bristle. The meaning, therefore, is exactly the opposite of that given by DE VRIES." If the reader will kindly look up my book at the page quoted by DAVIS, he will find that I have translated "sétacé" by "fadenförmig."

[24] The Mutation Theory, Engl. ed. 1:442, note 2.

[25] Bull. Torr. Bot. Club *op. cit.* p. 527.

The plant which POURRET called *O. grandiflora* Lam. is represented on our pl. XVIII. It agrees wholly with the present *O. Lamarckiana* Ser., and in all respects. It was fastened on its sheet by the clerk of POURRET and consists of two flowering spikes and two separate flowers. The stigma lobes are seen spread above the anthers in the normal way. The specimens were picked at the beginning of the flowering period and bear no fruits; obviously they were main spikes. They will be recognized at once as *O. Lamarckiana* by anyone who has seen living cultures of this species. As I have quoted in my *Mutation theory* (*loc. cit.*), SPACH has written on this sheet "*Onagra vulgaris grandiflora* Spach," which remark also proves the identity with *O. Lamarckiana* Ser. The printed label says "Collection de l'Abbé POURRET, extraite de l'herbier légué par M. le Dr. BARBIER en 1847." The main spike measures about 40 cm., the smaller one about 20 cm.

In my book I have also referred to a specimen of *O. suaveolens* Desf. At that time I did not know the Alabama species and believed that *O. suaveolens* Desf. and *O. grandiflora* Ait. were synonyms, as almost all authors did. Therefore I used the two names promiscuously. Last summer, however, I cultivated, side by side, *O. suaveolens* Desf. from Fontainebleau, collected by Dr. BLARINGHEM, and *O. grandiflora* Ait. from Castleberry, Alabama, collected by myself with Mr. BARTLETT. They proved to be wholly different species.[26] So far as I know, the large-flowered Oenotheras, which are now relatively common in the western departments of France, all belong to *O. suaveolens* Desf., at least all the specimens and cultures on which I based my opinion in 1901 did. The specimen of the Muséum d'Histoire Naturelle, which I referred to especially, has been described by DAVIS from a photograph which is reproduced on *pl. 39* of his paper. DAVIS, who did not know the *O. suaveolens* as a separate species, called it the flotsam of the herbarium (p. 529); it is, on the contrary, the authentic specimen of DESFONTAINES, bearing on the label the name *suaveolens* written by DESFONTAINES himself. The smaller plant, fastened on the same sheet, has another label, saying only *O. grandiflora*, and seems to me to have been fastened on this sheet subsequently. The

[26] L'*Oenothera grandiflora* de l'herbier de LAMARCK, *loc. cit.*

larger one, however, corresponds exactly with the species which is now growing in many thousands of specimens near Samois on the eastern limit of the Forêt de Fontainebleau, where I visited the different stations with Dr. BLARINGHEM in October 1913. The long fruits and the thick flower buds do not leave the least doubt concerning the identity of this specimen.

The most interesting discovery in this field of historical research, however, is that of a specimen of *O. Lamarckiana* Ser. in the collection of MICHAUX, described recently by BLARINGHEM.[27] I had the advantage of studying this sheet myself, when I visited Paris in October 1913. The printed label says "Herb. Mus. Paris, Herbier de l'Amérique septentrionale d'ANDRÉ MICHAUX." There is no further indication of the locality and no name. The specimen is a main spike, picked in the beginning of the flowering period, and without fruits (pl. XIX). It is excellently preserved and corresponds in all respects to my cultures of *O. Lamarckiana* Ser. The lobes of the stigma are seen to be widely spread above the anthers. The flowers and flower buds are exactly those of the present species.

ANDRÉ MICHAUX died in 1802, after having traveled during twelve years through the eastern United States from the Hudson River to Carolina. His celebrated collection constitutes one of the best sources of our knowledge of the flora of those parts of America at the end of the eighteenth century, that is, of the same period in which LAMARCK published his volumes of the *Encyclopédie*. His herbarium is at present at the Muséum d'Histoire Naturelle at Paris, and his plants were described after his death by his son FRANÇOIS ANDRÉ MICHAUX in a book entitled "ANDRAEAS MICHAUX, Flora boreali-americana, sistens characteres plantarum quas in America septentrionali collegit ANDRAEAS MICHAUX."[28] MICHAUX had the habit of collecting seeds of as many species as possible, besides his herbarium specimens, and of sending them to Europe to be sown.

[27] BLARINGHEM, L., *L'Oenothera Lamarckiana* Seringe et les Oenothères de Fontainebleau. Rev. Gén. Botanique **25**:1914.

[28] Editio nova, 1820, Paris. The genus *Oenothera* is dealt with in vol. I on p. 214; the plant is given under the name of *O. biennis*. For the ground covered by his travels, see the preface and the article of BLARINGHEM.

This beautiful specimen proves that *O. Lamarckiana* Ser. was a component of the flora of the eastern part of Northern America at the end of the eighteenth century, and that it has come down to us as completely unaltered as may be shown by old herbarium specimens. Moreover, it tends to make it at least very probable that the European strains, or at least some of them, are derived from the importation of seeds by MICHAUX. The specimen *A* in the herbarium of LAMARCK, designated as "d'Amérique sept.," probably belonged to this same strain.

The exact situation of the locality where MICHAUX collected this specimen is, of course, unknown. Much stress is laid by many authors upon the fact that no wild station for *O. Lamarckiana* has been discovered lately in any part of the United States. This argument evidently loses the main part of its weight when we know that it was observed by such a well known botanist as MICHAUX. Moreover, this situation is not peculiar to *O. Lamarckiana;* on the contrary, the same condition prevails for the other European species, *O. biennis* L., *O. muricata* L., and *O. suaveolens* Desf., whose original stations in the United States and Canada have not been rediscovered. Even *O. grandiflora*, which is known to occur in Alabama in different localities, is observed there to grow on cultivated soil only, especially on old fields of corn and cotton, and no one knows whence it came. Therefore, if our present ignorance of the origin of *O. Lamarckiana* is adduced in order to throw a doubt on its reality as a good species, the same doubt is attached to its nearest allies, and, in fact, to all the dozens of elementary species of the group *Onagra* which are now being found wild on waste fields and along roadsides all through the United States. Autochthonous stations are not known for any of them.

A most valuable contribution to the clearance of the historical data concerning the origin of *O. Lamarckiana* Ser. has been brought forward by DAVIS in his criticism of the alleged Texan origin of the present cultivated strain. This was introduced into the trade by Messrs. Carter and Co. of High Holborn in the neighborhood of London, about the middle of the last century. These horticulturists offered the seeds as coming from Texas. But, since then, no botanist is known to have seen the plant in that state, and DAVIS

suggests (p. 523) that the statement might, perhaps, have been caused by a mistake.[29] Now, it is well known that such details are, as a rule, given more in the interest of advertising than in that of pure science. Moreover, no horticulturist likes to offer for sale seeds with the announcement that the same form may be found as a wild flower in his own country.

O. Lamarckiana has been, for many years at least, a component of the flora of England, growing in many localities, especially on the sand dunes along the coast. The most universally known station is that of St. Anne's on the Sea, near Liverpool, which has been studied by BAILEY, GATES, and other botanists, and where the species occurs in thousands of specimens. DAVIS received seeds from different English stations and recognized the plant in the cultures derived from them (*op. cit.* p. 237). In Lancashire the species locally grows together with *O. biennis* L., exactly as it does in the sand dunes of Holland. In such cases it produces hybrids such as I have described under the names of *laeta* and *velutina*, and as DAVIS has isolated as small-flowered races from those English localities (p. 237).

Now, if we agree with DAVIS that the seeds of Carter and Co. were derived from some English station, the probability at once arises that these English stations themselves owe their origin to the introduction of seeds from America, either by MICHAUX himself or by some other botanist of the same period. The history of the species would then become a very simple and clear one. In this respect it becomes of interest to look at the figure published in 1807 in SMITH'S *English Botany* (vol. VI. *pl. 1534*).[30] According to the description accompanying this plate, the "specimen was gathered on the extensive and dreary sand banks on the coast a few miles north of Liverpool, where millions of the same species have been observed by Dr. BOSTOCK and Mr. JOHN SHEPHERD growing perfectly wild and covering large tracts between the first and second range of sand hills." In this same locality *O. biennis* L. and *O. Lamarckiana* are now growing in the same abundance of individuals, partly separated and pure in different valleys and

[29] See DAVIS in New Phytol. 12:234. 1913.

[30] Cf. DAVIS, *op. cit.* p. 532.

partly in mixtures which are known to contain also their hybrids. The specimen of 1807 is designated *O. biennis*, but both the flowers have the lobes of their stigma above the anthers, which is a differentiating mark of *O. Lamarckiana*. Moreover, it is the only decisive detail, all other characters of the figures applying equally to both species. If it is allowable to trust to this detail, we should be entitled to conclude that the station of Liverpool contained both forms as early as 1807, even as it is known to do at the present time. In this case, *O. Lamarckiana* must be assumed to have been introduced into England about the time of MICHAUX and LAMARCK, and a common origin for the specimens of their herbaria and the wild stations in England becomes highly probable.

The strain of Carter and Co. has been identified by LINDLEY as *O. Lamarckiana* Ser., and the high authority of this eminent botanist confirms my own determination of the same strain, made by comparing it with the authentic specimen of LAMARCK.[31]

At all events, the adduced facts indicate a very simple history of our species, which has come down to us unchanged, so far as we know, from the original American habitat.[32] There is no reason to suppose that it originated as a garden plant, and none at all to subject it to all the doubts ordinarily brought forward against the purity of descent of horticultural forms in general, simply on the ground that some garden plants are of known hybrid origin. *O. Lamarckiana* has remained unchanged through more than a century, and has kept as true to its type as any good wild species. "It is exceedingly fortunate," says DAVIS (*op. cit.* p. 527), "that the plant which serves as the type of *Oenothera Lamarckiana* Ser. should have come down to us so well preserved that there is scarcely a doubt of its identity." But the identity is with the species as it is still known under that name. Whether the species

[31] DAVIS says (*op. cit.* p. 531) "the identification by LINDLEY of these plants with *O. Lamarckiana* Ser. was undoubtedly incorrect," but he does not give any reason for this assertion.

[32] DAVIS says (*op. cit.* p. 530) "that *Lamarckiana* has come down to us greatly modified, that its parentage is far from pure, that it is in fact of hybrid origin." This assertion, which is not based upon any facts, is clearly contradicted by the preservation in excellent condition of the three specimens of LAMARCK, POURRET, and MICHAUX, not known to DAVIS.

was in the same condition of mutability at the time of its first appearance as it is now, is of course a different question.[33]

Summing up the results of this historical investigation, we may say:

1. *Oenothera Lamarckiana* Ser. is represented by specimens in the herbaria of LAMARCK, POURRET, and MICHAUX (pls. XVII–XIX), and is, so far as this material enables us to judge, at the present time exactly the same plant as it was at that period. It has come down to us, through more than a century, as unaltered and as constant as true species usually do.

2. It has been a component of the flora of the eastern United States, where MICHAUX collected it and whence LAMARCK derived his specimen.

3. At the present time it is a component of the flora of England, and is as well established in that country as is *O. biennis* in different parts of Europe.

4. The strain which is now in cultivation, and which was introduced into the trade about the middle of the last century, was probably derived from some wild English locality, which itself may have come from an introduction into Europe of the seeds collected either by MICHAUX himself or by some other botanist of his period.

AMSTERDAM

EXPLANATION OF PLATES XVII–XIX

Plate XVII

Oenothera grandiflora Lam. (*O. Lamarckiana* Ser.): the authentic specimen in the herbarium of LAMARCK, two-thirds natural size, referred to as *A* in the text; in the left upper corner a bunch of flower buds of my culture of 1913, dried and pressed, is given for comparison, and photographed together with the main specimen.

Plate XVIII

Oenothera grandiflora Lam. (*O. Lamarckiana* Ser.): the specimen in the herbarium of Father POURRET, one-third natural size; on the label is written *Onagra vulgaris grandiflora* Spach.

[33] Über die Dauer der Mutationsperiode bei *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. **23**:382. 1905.

OENOTHERA LAMARCKIANA SER.

HERBARIUM OF LAMARCK

OENOTHERA LAMARCKIANA SER.

HERBARIUM OF FATHER POURRET

OENOTHERA LAMARCKIANA SER.

HERBARIUM OF ANDRÉ MICHAUX

Plate XIX

Oenothera Lamarckiana Ser. in the "Herbier de l'Amérique septentrionale" of ANDRÉ MICHAUX, collected about 1800 in the eastern parts of the United States: *A*, top of spike photographed and reproduced about natural size; *B* and *C*, the whole specimen of MICHAUX, consisting of two parts, reduced about one-half; all three figures photographed for me by Dr. L. BLARINGHEM; in the reproduction the narrow bands of paper used to fix the specimen to its sheet and seen on the photographs have been omitted.

THE SPUR SHOOT OF THE PINES

ROBERT BOYD THOMSON

(WITH PLATES XX–XXIII AND TWO TEXT FIGURES)

Introduction

The deciduous spur shoot, with its limited growth and persistent whorled needle leaves, is the distinguishing vegetative feature of the genus *Pinus*. This structure has been generally regarded as a specialization, the more primitive form of the foliage being indicated by the single spirally arranged leaves which occur on the seedling and in some forms on the adult plant after injury. JEFFREY, however, has raised the question recently of the primitive or specialized character of the fascicled foliage of the pines in his work on the phylogeny of the conifers. He states (**15**, p. 331) that the spur shoot is "a primitive attribute of the coniferous stock" which "has persisted at least in a vestigial form, in connection with the reproductive apparatus, long after it has disappeared, or almost disappeared, in the vegetative axis of the living conifers, with the exception of the very ancient genus *Pinus*." This view is so entirely at variance with so many foliage features, in both the living and fossil forms, that it is difficult to see how JEFFREY could have "cast the balance of evidence" in favor of it. Since, however, he makes much of this spur shoot argument in presenting his case for the ancestral position of the Abietineae among the other conifers, it is desirable to direct attention at least to the most important features of the evidence which is opposed to this view. The writer (**27**) has already stated, in a brief and general way, some of these features, in a paper dealing with the relative antiquity of the Abietineae and the Araucarineae, from the standpoint of their anatomy. New material, however, has recently come to hand which has prompted this more extended treatment of the subject. The literature has also been thoroughly canvassed for information on the spur of the pines.

Of the conifers there are four genera with fascicled leaves: *Cedrus*, *Larix*, *Pseudolarix*, and *Pinus*. In the first three of these

the leaves are numerous, while in *Pinus* they are much more restricted in number, not more than 8 having been recorded up to the present. In the former, too, the number is indefinite and the leaves are spirally arranged, while in *Pinus* the definite cyclic arrangement has been established. A parallel to this is seen in the angiosperm flower, where the lower forms of both monocotyledons and dicotyledons have an indefinite number of floral parts in a low spiral, while in the higher forms the number is definite and the arrangement cyclic. The spur shoot of *Pinus* is deciduous in the second to the twentieth year (ELWES and HENRY **7,** p. 1002), and its leaves fall with it, remaining permanently attached. In the other genera it is the spur shoot which is persistent, and the leaves are cast either annually or in the second to the fifth year. The small and more or less definite number of persistent and whorled needle leaves and the regularly deciduous character of the spur shoot are features which render this structure in the pines very unlike the ordinary branch and also unlike the spurs of the other forms, which differ from an ordinary branch only in their limited primary and secondary growth. The features that will receive attention in this paper are such as indicate the branch character of the spur in *Pinus*.

Number of needles

The number of leaves in the fascicles of the pines, appearing on first sight constant, and being, as ENGLEMANN says (**8**), "the most obvious distinctive character," has been extensively made use of in their classification. He states (**8,** p. 161) that "the sections of 2-leaved, 3-leaved, and 5-leaved pines were the only ones known to the older botanists"; to these were added two other sections "by LINK (*Linnaea*, 1841), one with 2 or 3, the other with 3 or 4 leaves in a sheath." Subsequently forms with single leaves and others with 3–5 leaves in the fascicle had to find a place. Numerous exceptions to this classification have also been recorded. KRONFELD (**16,** p. 68) gives a summary of the variation in many different species observed up to the date of his article. He cites, for example, the occurrence reported by REICHARDT of 3, 4, and 5 needles in *P. silvestris*, which is normally bifoliar, and also of 3, 4, and 6 in

P. Cembra, which has usually 5 to the fascicle. To Dr. G. R. SHAW I am indebted for another reference to the 3 to 5-leaved condition in *P. silvestris* (see KIRCHNER, LOEW, and SHROETER, Lebensg. d. Blütengepfl. Mitteleur. I, 187) and for one to *P. halepensis*, a bifoliar form which may bear 3, 4, or 5 leaves (see MATHIEU, Fl. Forest, ed. 4, 608). In *Gardeners Chronicle* of 1852 (p. 693) an anonymous writer speaks of having raised a variety of *P. austriaca* (normally bifoliar) with 3 leaves. He speaks of these fascicles as being all over the tree, which was about 10 feet high and very dense. The same writer says: "I also find *Pinus Hartwegii* still halting between two opinions between a 3-leaved and a 5-leaved fir. . . . . *Pinus mitis*, *P. variabilis*, *P. muricata*, and others are too well known in their similar tendencies to need remark. My *Pinus insignis* has many a group of 4 leaves, instead of the prescribed 3." In *P. macrophylla* he found fascicles with 6 and 7 needles quite common, even some with 8. SHAW himself (**26**, p. 6), in his description of the pines of Mexico, encountered so much variation in four of the nut pines (*P. cembroides*, *P. monophylla*, *P. edulis*, and *P. Parryana*) that he said: "I find it impossible to separate these specifically, their cones being identical and the number of their leaves inconstant." The leaves in the foregoing instance varied between 1 and 5. He has also recorded (p. 23) a great variation in single species. Of *P. Montezumae* he says: "Trees bearing fascicles of 6, 7, or 8 leaves are quite common, but such excessive numbers are found usually on older trees and in favorable years. On young trees fascicles of 3 and 4 leaves may be found, but in all cases fascicles of 5 predominate." Of *P. ponderosa* the same author states that the leaves are in fascicles of 2–5, but has found fascicles of 6–8 on mature trees. *P. Teocote*, *P. patula*, and *P. Lawsoni* agree in having usually 3 to the fascicle, but the first two have occasionally 4 or 5, while this is more usual in the third. In *P. leiophylla* the conditions are evidently reversed, since SHAW (p. 13) says that the leaves are "in fascicles of 5 or of 3 and 4." SARGENT (**24**, p. 119) states of *P. serotina*: "The leaves are borne in clusters of 3 or occasionally of 4 on vigorous young shoots," while of *P. heterophylla* he says (p. 157): "The leaves are borne in crowded clusters of 2 or 3, the 2-leaved clusters being most common

on young vigorous trees and on fertile branches." In *P. Pinea*, which usually has the leaves in pairs, ELWES and HENRY (**7**, p. 1119) state that "on well developed vigorous branches, a few of the leaves are sometimes in clusters of threes." Of *P. Torreyana*, whose adult leaves are in fives, they also state (p. 1065) that "on young plants the leaves are frequently in clusters of 3 and 4." BORTHWICK (**1**) has described a tree of *P. Laricio* 12 years old with 2, 3, and 4 leaves to the fascicle. The quadrifoliar spurs were found only at the top of the tree, which was of very vigorous growth.

The variations in the number of leaves in the pines have been recorded practically as isolated instances and have not been correlated. As they stand, they show that the spur shoot is not so definite and so specialized a structure as has been supposed, but that it is more in the nature of a branch with an indefinite number of foliage leaves. When, however, one looks farther into the variations from the standpoint of the spur being ancestrally a branch, it is evident that the fascicles with supernumerary needles should be found in the more primitive parts of the plant: on the seedling, on the fruiting branch, after wounding, etc. My own investigations have been along these lines, and though they do not completely correlate the cases reported, they go very far toward doing so and afford one important line of evidence of the branch character of the spur shoot.

Fig. 1 is of the upper part of a 3-year-old seedling of *P. Strobus*.[1] Primordial leaves are unusually persistent on this plant, and may be seen among and below the three spurs with the rubber bands around their leaves. Brown scale leaves, however, replace these green seedling leaves around the base of each fascicle just as in the ordinary spur. The middle spur bears 15 leaves, the one to the right 11, and the one to the left 7. Fig. 2 is of a seedling of the same species, one year older. The main axis in this case made a comparatively short growth the last season and bears 6 fascicles. The central one of these has 9 leaves, the one to its right 10, the two below these 7 each, the lowermost to the right 5 large and 2

[1] I cannot determine absolutely that these and the other young forms are *P. Strobus*. It is possible that they are *P. excelsa*, but, since some consider the two species as geographical varieties, the matter is unimportant from the present standpoint.

small, while the lowest to the left has 6 equal-sized needles. This plant was slightly wounded a year ago last spring in connection with some work a student is doing along another line. It was not injured, however, in such a way as has been found in other cases to interfere with the number of needles. Again, several sister plants similarly injured did not show any reaction. It is probably better to consider this case a "sport," just as in the case of the 3-year-old plant, which had not been injured in any way so far as could be determined. In only one instance have I found younger plants than these with extra leaves in their fascicles; one seedling from a dozen or so of *P. flexilis*, which are now in their second year, has a fascicle with 6 needles. It is among the first formed fascicles of the seedling and at the top of the second season's growth.

It is more usual to find the spurs poorly developed when they first appear on the seedling, which is generally in its second year, though in some species they are delayed till the third year, or even later. This feature shows itself especially in species which have normally more than two leaves in the mature condition. For example, HEMPEL and WILHELM (11) refer to *P. Cembra* seedlings two years old as having trifoliar spurs, though the adult plant is normally quinquefoliate. I have also found trifoliar spurs common in *P. Strobus* when fascicles first appear on the seedling. Some spurs here are even bifoliar. In these reduced spurs the needles apparently come right out of the stem, the shoot axis, if any be present, being imbedded in the tissue. These fascicles also are usually devoid or almost devoid of bracts. In *P. silvestris* I found in 35 seedlings two years old only one example of a trifoliar spur. This was on the most vigorous of the plants. In plants a few years older, which had attained to considerable vigor of growth, I could scarcely find one without trifoliar spurs unless it was a weakling. At first the occurrence of these reduced fascicles on the seedling seemed entirely at variance with the view that the spur shoot of the pines is a branch. It is a feature, however, which is shared by other spur shoot-bearing plants. In *Ginkgo*, for example, when the spurs first appear, about the third year, they bear only 1–3 or 4 leaves, and gradually gain in number as they advance in age until

they attain their mature condition. This is also true of the other fascicle-leaved conifers, sometimes only one or two needles developing in the season that the spurs appear. There must thus be some common physiological reason underlying this feature, and no doubt it is the well known lack of vegetative vigor in the seedlings of the conifers generally. During the first few years they are busy establishing a root system and there is little stem growth. Foresters and nurserymen know this early critical stage in the life of the conifers only too well. The growth in these early years could be measured in inches, while in later years it would require feet.

I have examined older forms, 6–15 years old, of a large number of different species belonging to all the different sections of the pines, and have found supernumerary needles quite common, especially on vigorous specimens. On the main axis of one unusually sturdy plant of *P. Strobus*, a plant which had made at least a foot and a half of stem this year, and this stem fully three-quarters of an inch in thickness at its base, there was a spiral sequence of fascicles with 6, 7, 8, 9, and 10 needles. Fig. 4 is of one of these. The supernumerary needles have been surrounded by a rubber band, and it will be seen that they show a spiral gradation in length. This is a feature which to a less degree is sometimes shown by the 5 original needles themselves. It is indicative of the concealed spiral arrangement of the leaves on the spur. This feature, I find, was observed long ago by MEEHAN (**22**), and its significance noted. The series of spurs referred to above occurred on the lower part of the year's growth. It is more usual, however, to find spurs with extra needles near the apex of the season's growth. I have found many instances of this in a mixed plantation of pines about 8 years of age, which consisted of *P. Strobus*, *P. silvestris*, and *P. Banksiana*. Of the white pine there was a large proportion of vigorous specimens with supernumerary needles. The Banksian pine showed few instances, but in the Scotch pines they were very numerous. I should think fully 75 per cent of these had several (3–6 or 7) trifoliar spurs at the apex of the year's growth. These trifoliar spurs could be traced for two to three years previously at the corresponding places on the stem. The occurrence of trifoliar spurs in this species at the branch region was observed by

the anonymous writer in *Gardeners Chronicle* of 1852, to whom reference has already been made. He says of these spurs in *P. silvestris:* "I have gathered 8 or 10 examples round one bud alone," and adds "on the *macrophylla* the examples are very numerous," evidently intending it to be understood that the abnormal fascicles of this species, which he has described with 6–8 needles, were also found in the branch region. I have observed in *P. excelsa* 6–7 needles in the same position, in *P. parviflora* 6, and in *P. virginiana* 3. The first two of these are normally 5-foliate, while the third is 2-foliate. In *P. Jeffreyi*, which is normally 2–3-foliate, I have found on plants of about 8 years of age spurs with 5–6 needles; these were often in a terminal position (see fig. 13, where a branch has originated from such a spur). In all cases it is more usual for the extra numbers to appear on the main axis than on branches, though I have found them on the same plant in both places. I have examined fruiting branches in the case of *P. Strobus* and *P. excelsa* only, and have found several instances of 6-needled fascicles on these.

This normal production of supernumerary leaved fascicles, as it may be considered, is interesting, but of much greater interest is their traumatic production. The past summer, Mr. J. R. FRYER was experimenting with white pine along this line and succeeded in producing on young trees, about 15 feet high, fascicles of 6–8 leaves, in one instance 11. He cut the young growth from vigorous branches and main axes in the latter part of May, and when new growths arose they had in some cases the extra needles in the fascicles. In *P. excelsa*, at about the same height, I found in the middle of July many such cases, where the terminal bud had been injured in the early spring (probably by the pine shoot beetle, *Hylesinus piniperda*) when the fascicles were beginning to develop. The wounding caused numbers of these fascicles to develop extra leaves. Fig. 3 gives a fair illustration of the tufted appearance of these shoots and shows three fascicles with 9–11 needles (see also in fig. 10 the central fascicle). In some instances the number of leaves reached 15. In *P. parviflora* I have found on a young tree fascicles of 6–9 needles. These were near the top of the main axis, which had been slightly wounded lower down. Even in the

single-leaved pine, *P. monophylla*, wounding increases the number of needles to two. Figs. 5 and 9 are from a young tree which was normally monophyllous. Both twigs were injured just as the leaves were starting to develop. On the first, three bifoliar spurs have been produced, and on the second, one. I have not observed an increase in the number of needles by wounding in any other forms, but it is probably of quite general occurrence in the pines.

Before leaving the subject of the number of leaves in the fascicle, a peculiar and probably a specialized condition, which has been reported in several species, must be referred to. In *P. Nelsoni*, SHAW (**26,** p. 8) states that the leaves are "connate in fascicles of 3," and that this condition is found even in the seedling. In *P. Thunbergii* the leaves are in twos, while "in var. monophylla the two leaves in the cluster coalesce" according to ELWES and HENRY (**7,** p. 1143). These authors also refer to two other cases of fusion of the leaves; to CARRIÈRE'S (Conif. p. 398, 1867) description of a variety (*monophylla*) of *P. excelsa:* "each sheath with apparently only one leaf, all of the five leaves being welded together" (p. 1011), and to a monophyllous variety of *P. Strobus* described by TUBEUF in 1897, "a variety with the needles more or less cohering throughout their length, and forming a single needle" (p. 1026). It is necessary to distinguish this spurious monophyllous condition, a result of compounding, from the truly single-leaved condition in the one species, *P. monophylla*, which as MASTERS (**20**) has shown arises from the "arrested development of one of its two original leaves" (p. 126).

Scale and primordial leaves

Below the persistent whorled needle leaves on the spur shoots are spirally arranged scale leaves, which are homologous with the similarly though more laxly arranged scale leaves on the ordinary branches. They are either persistent or deciduous. On seedling stem and branches scale leaves are replaced by the so-called primordial leaves, which are a prominent feature in the pines. These seedling leaves, as COULTER and CHAMBERLAIN (**5,** p. 222) have noted, are of simpler structure than the whorled needles. There

are gradations in structure, however, between the two types of foliage. BORTHWICK (**1**, p. 153) refers to this feature in his description of the supernumerary needles of *P. Laricio*, to which reference has been made. He says that "the fourth needle, ... although it shows some of the primary leaf characters internally, still, in outward appearance, it resembles the normal acicular leaves, exhibiting in fact a transition stage between the two." I have found very complete series of transitions in form between both scale and primordial leaves, and also between these and the whorled needle leaves. The latter is well indicated in fig. 10, where the upper spur (5-foliate) has proliferated into a branch with primordial leaves. It is possible here to tell the spur leaves from the others only by their low spiral arrangement and by their slightly triangular rather than flat form. In the fascicles illustrated in fig. 3, some of the upper bracts have been modified into green seedling-like leaves. The needles of these fascicles, too, are flatter, shorter, and more like the primordial type. This is especially true of the needles of the fascicles in the younger plant shown in fig. 1. More definite reference to these points will be made in a future paper dealing with the internal structure. The morphological evidence, however, seems sufficiently clear that the spur shoot leaf is only a specialized primordial leaf, just as the scale leaf is also a modification of it.

The transformation to both types of foliage occurs at somewhat different stages in the life of the seedling of various pines. Of *P. monophylla*, SARGENT (**24**, p. 51) says: "primary leaves are the only ones produced during the first five or six years in the life of the plant"; while BRITTON (**3**, p. 14), in referring to this feature in *P. cembroides*, states: "juvenile leaves of this and other nut pines are produced for the first five years or more, often to the exclusion of all others . . . . the new ones shorter as the buds of the fascicled, needle-shaped leaves develop in their axils." MASTERS (**21**, *fig. 1*, p. 586) has figured the persistent primordial leaves of one of these, *P. Parryana*. He previously figured those of *P. Pinea*, a form in which he notes that they were observed long ago by LINNAEUS (MASTERS **19**, p. 258 and *fig. 8*). Of the last mentioned species, ELWES and HENRY (**7**, p. 1120) state that "the primary leaves are produced . . . . for several years, in mixture,

after the first season, with the adult geminate leaves." LLOYD's (**18**) attention was attracted to the great persistence of the primary leaves of a young plant growing in the New York Botanic Gardens. In *P. canariensis* the leaves persist even longer than in *P. Pinea*. In *P. rigida* they are also very persistent. In the seedlings of most forms, however, the primordial leaves do not last beyond the second or third year.

Primordial leaves are not, however, restricted to the seedling. According to MASTERS (**19,** p. 258), "they occur frequently on the lower part of the shoots of the year, as in *Pinus sabiniana*, *Pinea*, *silvestris* (sometimes), and other species"; also "in some cases, on the branches or stalks immediately supporting the cones, as in *Pinus excelsa*, etc." In *P. monophylla*, ELWES and HENRY (**7,** p. 1056) have noted that "in cultivation adventitious shoots bearing flattened primordial leaves are occasionally produced on the lower branches." SHAW (**25,** p. 206), in speaking of the "summer" growth of certain southern pines of the United States, says: "this growth, in the summer, differs from the spring growth not only in its less development, but also in its *green* bracts, which, not being required for the protection of the winter bud, assume more or less completely the size, color, and character of the primary leaf." SARGENT (**24,** p. 4) states that: "*Pinus rigida* and *Pinus echinata* are the species of the United States which generally bear primary leaves on branches, or produce freely shoots from the stumps of cut trees. These shoots, which are clothed with primary leaves, grow vigorously for a few years, and then usually perish." ENGELMANN (**8,** p. 163) speaks of this feature in *P. inops*, *P. rigida*, and *P. canariensis*. In the last mentioned, it is very prominent in some instances. Miss COOLEY (**4**) refers to and figures a tree at Naples which was practically clothed with shoots bearing primary leaves. A young specimen of the same species in the New York Botanic Garden shows many reversions to primary foliage. Whether in these instances all the reversions may not be the result of injury is uncertain. Wounding does give a response in the case of the production of resin canals for several years after the injury, especially prominent being the response in young twigs which are formed subsequently to the wound, and it is probable

that the extent of the primary leaves due to wounding is much greater than at first appears.

The possibility of reviving the primary type of foliage by wounding must be fairly common in the pines, for in addition to the ones that have been mentioned, MASTERS (**19**, p. 258) refers to their production after injury in *P. edulis*, *P. Parryana*, and *P. Khasyana*. The past summer I have observed it in ten or more species: *P. canariensis*, *excelsa*, *halepensis*, *Jeffreyi*, *Laricio* and var. *austriaca*, *monophylla*, *Pinaster*, *Pinea*, *ponderosa*, *Thunbergii*, and *tuberculata*. LLOYD, moreover, has produced the primary type of foliage experimentally in *P. ponderosa*. He states (**18**, p. 101; see also original article, **17**) that "shoots, which normally would bear only thin, brown, papery scales, namely the shoots which bear the male or pollen-bearing cones, may be made to produce true primordial leaves by the mere pruning away of the upper part of the shoot early in the spring." HOCHSTETTER (**12**) has gone farther, and has succeeded in fixing the juvenile foliage in *P. Pinea* and *P. canariensis* by cuttings, having accomplished in this specialized genus of the Abietineae what is common practice in the Cupressineae. He states (p. 367): "Stecklinge von *Pinus canariensis* und *Pinea*-Sämlingen, im zweiten oder dritten Jahre abgenommen, wachsen leicht an, verharren in der Primordial-form und bilden bläulichgrüne Büsche mit spiralig einzeln gestellten Nadeln von unvergleicher Schönheit." Unfortunately, these "incomparably beautiful" shrubs are but short-lived. Had they succeeded better and become disseminated through horticulture, they would have afforded a convenient and valuable demonstration of the primary type of foliage of the pines.

In some seedlings of *P. Strobus* in the third year I have found a reversion to primordial leaves where no wounding could be detected. The leaves, for example, shown on the branch above and to the left of fig. 11, though broader and more closely set than usual, are primordial leaves produced after the plant had formed spur shoots. Such leafy branches may even originate from a spur shoot, three stages of differentiation being shown in the figure. To this point, however, reference will be made again. MASTERS has observed (**19**, p. 258) in *P. rigida* and *P. silvestris* that if the main axis is

injured slightly above the cotyledons the branches which are produced in response to the wound bear only primordial leaves. He considers that this doubtless occurs in many others. From these facts and the stump sprouting, which has been referred to above, it seems probable that in all cases the epicotyledonary region, in the young plant especially, reverts more readily to the primordial type of foliage than the upper parts of the stem, and that what seems more or less normal here and, in some cases below the cones, can be made to occur in other parts by wounding. PHILLIPS (**23**) has recorded some observations bearing on this point. Speaking of the sprouting of *P. chihuahuana* after injury by cattle and fire, he says (p. 385): "typical sprouting . . . . is confined to trees under 5 cm. in diameter (measured at breast height), which send up most of the shoots from the root collar or the first 30 cm. above ground." This power of stump sprouting, as it is called, also decreases with the size of the stump: "Not a single case was found where the stumps of trees smaller than 7.5 cm. in diameter had failed to produce thrifty sprouts, and fully 30–50 per cent of the stumps of trees up to 22.5 cm. in diameter had produced very thrifty sprouts, most of the fail stumps occurring between the 15 and 22.5 cm. classes" (pp. 386–387).

Proliferation of the spur shoot

The spur shoots, like ordinary branches, arise either in the axils of primordial leaves or, when these have been replaced on the stem by scale leaves, in the axils of the latter. Unlike the branch, however, the spur shoot of the pines increases neither in length nor in diameter after the first few weeks, though it may remain on the tree with leaves green and apparently functional for many years. Thus, primary meristem and cambium are normally inactive through by far the greater part of the life of the spur shoot. This limited growth of the spur shoot and the production by it of only one set of assimilatory leaves which are persistent, not even detached on the fall of the shoot, are the distinguishing features of the spur of the pines. In the other fascicle-leaved conifers, a new set of leaves is added to the spur shoot each year for many years (cf. *Ginkgo*). There is thus a slight annual increase in length, the

spur shoot elongating, much after the fashion of the cycad stem, enough to accommodate each new set of leaves. The "spurs" in these forms may attain a length of an inch or more on the older branches; they gradually become shorter toward the younger parts, and on the season's growth primordial leaves alone may be present. These persist in *Cedrus* for two to three years. The occurrence of these primordial leaves on the season's growth are a contrast to the condition in the pines, where only scale leaves are normally produced. In *Cedrus* the fascicled leaves themselves persist for two to five years, while in *Larix* and *Pseudolarix* they are shed annually. In the pines they are indefinitely persistent, falling with the spur. Undoubtedly the persistent habit is the ancestral one for the conifers, having been overcome in two ways, by the deciduous leaf and by the deciduous branch, as the writer has tried to show in a recent article on the Araucarineae (**27**).

The spur shoots of the three genera referred to, in addition to having the power of making a short yearly increase in length, have also the power to a marked degree of forming ordinary branches as occasion arises. The main axis may originate from a spur shoot, usually the terminal one, but if this is injured, any of the proximals may assume its function. Lateral branches also arise normally from spur shoots, especially from the younger ones. When, however, a branch is injured, they may arise from old spurs. The spur shoot of these three genera retain to a marked degree the power of branch formation. It remains, however, to a large extent latent unless called into activity by the needs of the plant. This dual power of the spur shoot either to produce a branch or to continue the growth of the fascicle as such is an indication of the genetic relationship of the branch and spur shoot. One would scarcely expect such a feature in the pines, where ordinarily in the mature condition not even a rudiment of a bud can be discerned amid the closely set needles of the fascicle, and where, too, only the one set of leaves is produced and the axis neither increases in length nor in diameter after it has formed these.

On the contrary, however, proliferating spur shoots similar to those in the other genera are of very general occurrence in the pines. They do not occur so abundantly nor so normally as in

the other genera, and have escaped observation to a great extent. Several instances, however, are on record. ENGELMANN (**8,** p. 167) says: "in exceptional cases and as a monstrosity the leaf bundles may become proliferous, the branchlet which bears the secondary leaves elongating and forming a regular branch." MASTERS (**19,** *fig. 9* and p. 267) figures a pine, with two needles, in which the fascicle is "prolonged into a shoot with primary leaves and leaf buds." Neither ENGELMANN nor MASTERS mentions the species concerned, nor in either case do they indicate the conditions which have induced the proliferation. DICKSON (**6**) and MEEHAN (**22**) both observed that in *P. silvestris* proliferation occurred as a result of injury. DICKSON's specimen was a twig, the extremity of which had been destroyed. He says (p. 260): "the development of these buds is stronger the nearer their position to the seat of injury." The lower ones are merely closed buds, but the upper ones "develop well marked foliage leaves, and, in the very strongest ones, these foliage leaves have secondary bifoliar spurs developed in their axils." In the development of foliage leaves spirally arranged "on the prolonged axis of the stimulated spur," DICKSON notes "a reversion to the early or unspecialized condition." MEEHAN's (**22,** p. 82) specimens were Scotch pine that had been "headed back." Previous to his observation of these proliferating spur shoots, he had been so influenced by VON MOHL's work on *Sciadopitys* that he was inclined to consider the fascicled needles of the pine as cladodes. He now subscribed to the current view and recognized that the whorled needles are leaves and that the fascicle is an "arrested branch, having a dormant bud at the apex." BORTHWICK (**2**) has observed numerous instances in a plantation of *P. Laricio* and *P. silvestris,* and has studied the conditions under which they develop, as well as the character of the resulting branch. He considers that "the interfoliar bud develops only under the stimulus of an increased supply of nutriment," and instances several kinds of wounding which result in a greater advention of food material. In this he agrees with HARTIG's explanation of the development of dormant buds. He considers that the branch produced from the development of the interfoliar bud may bear either primary or fascicled leaves, "the results

varying with the conditions under which the buds are induced to develop and the general health of the tree at the time" (p. 157); the greater the supply of nutriment, the more likely it is that the proliferating branch will produce spurs, the primordial foliage occurring on those with the smaller supply. BORTHWICK has even referred to an economic aspect of the proliferation of the spur. He considers that the appearance of scraggy pine trees could be improved by a judicious disbudding process and a stimulation of the spurs to form branches.

It is in the seedling and in the young vigorous plant that I have observed most instances of proliferation, the occurrence of proliferating spurs following very closely that of supernumerary needles. This applies also to their common production in the mature tree by wounding.

The upper part of a seedling of *P. Strobus* at the beginning of its third year is shown in fig. 6. A branch with young spur shoots (this season's growth) has been developed from the interfoliar buds of four spur shoots of last season's growth. The central one of these will probably form the future stem. The big branch to the lower right of the photograph, whose leaves have been tied together, arose a year previously also from a spur. Above it is a normal fascicle which has not proliferated. The main axis below the leafy part had its end destroyed, as its dead stump shown against the small white slip indicates. Its lower branches, which were uninjured, bore only normal spur shoots, and it is possible that wounding has had something to do with the proliferation of the upper spurs. I found, however, in what so far as could be determined was an uninjured sister plant, one case of proliferation. In another, also apparently uninjured, I found a reversion to primordial leaves, which has been previously mentioned; though the large branch shown to the upper left of fig. 11 did not arise from a spur shoot, at least, if it did, no trace of the fascicle of leaves remains, yet to the right of the terminal bud there is a spur shoot with a small set of primordial leaves, while to the lower left of the figure two other fascicles are shown with smaller series, so small that they are practically green buds. This photograph was taken while the plant was in its winter condition. Two of these fascicles have since

developed into branches with both primary and secondary leaves. I have found similar proliferations on seedlings from the same plot, but could detect no injury except in one instance. The seedlings were all grown and carefully tended in the University Garden. Moreover, in both seedlings shown in pl. XX there are well developed buds in all the spurs except two (the lowermost of fig. 2), some of which will in the ordinary course of events grow next year into branches. In fact, the main axis will come from one of these in both instances, as it has done in the plant shown in fig. 6. One is so much larger than the others in each case that there seems no doubt of its power to produce the main axis.

On examination of older seedlings of other species, I found that branches had quite frequently arisen from spur shoots in certain plants, again not connected with any apparent injury. Among about 20 young plants of *P. virginiana* (?), several had proliferating spurs, and were vigorous specimens about 6 years of age. In fig. 7 the two leaves (marked with a single line each) inclose the terminal axis with a rosette of lateral buds at its apex. These two leaves have very broad bases. Below and to the right is a lateral bud coming from a spur shoot with three leaves (marked with 2 lines each). Two of these are also broad, but the third is much narrower. It is to be noted that this species has its leaves normally in twos. Below this spur shoot is one with two broad leaves (marked with 3 lines each) and a much smaller bud, below which again are spur shoots with smaller and smaller buds, until at the base of the shoot figured no trace of a bud could be discerned, even with a lens. During previous years certain of the branches also arose from spur shoots on this plant. In vigorous specimens of *P. Strobus*, about 8 years of age, chiefly from the plantation referred to before, but in the wild also, I have found that usually subsidiary branches occur below the normal whorl. These are smaller and in almost every instance derived from the proliferation of a spur. One of them at the end of its first season's growth is shown in fig. 8. It has normal secondary needles and is only one of several at the same node. Around the apex of the stem below the branch node, a number of this year's spurs have small buds which are ready to develop next year into similar branches. In a few specimens of

P. parviflora, I found numerous examples of similar proliferations. A large proportion of these branches formed in this way perish later, but some persist and develop normally. Sometimes in these species the spurs which will proliferate have an extra needle. In *P. silvestris* this is normally the case. In vigorous specimens the lower branches on the swollen branch node of this form come regularly from trifoliar spurs. Many of these branches persist, and I have also observed that sometimes the main axis comes from a spur, no special terminal bud being formed. This condition, however, is rare in the Scotch pine at the stage (about 8 years old) examined. In *P. Banksiana* in the same plantation proliferation was not so common as in the other two species,[2] but occurred under the same conditions.

FIG. 1.—*Pinus ponderosa* var. *Jeffreyi* (one-half nat. size): the main axis and a branch developed from spur shoots in a plant about 6 years old.

In some young plants of *P. ponderosa* var. *Jeffreyi*, I have found proliferation very common. These plants were about 6 years of age, and did not exhibit any special vigor of growth. Text fig. 1 shows the main axis and a branch, with some of the needles of the spur from which they arose attached to their basal regions. Others of these needles have become detached. In these plants there are normally only 3 needles to a spur. In the axial stem-producing spur shown above, 4 needles are still attached to the base, and the broken stumps of 2 others can be clearly seen. The branch spur has but 2 needles intact, but the stumps of 2 or 3

[2] Mr. C. H. MORSE, while on a visit to the government nurseries in Norfolk County, was good enough to examine Scotch, Banksian, and white pine, and reports that "proliferation is very abundant, especially in vigorous plants of *P. silvestris* 6 to 8 years of age, and fairly common in *P. Banksiana* and *P. Strobus* of about the same age."

others can be made out on the specimen, though not in the photograph. When one examines the insertions of these needles, they are seen to continue the spiral series of the scales above them, which are more developed than usual and more than usually persistent.[3] The spiral is a very low one in the case of the 3 lowest (the normal) needles, but comes out clearly in the supernumerary needles. In these, too, there is a very evident gradation in length, the leaves getting shorter the higher they stand on the axis. In fig. 13, for example, the 3 large (slightly spirally twisted) needles, though each is inserted at the base of a spiral series, are all about on a level. The other 3, however, are inserted at quite distinct levels. The shortest is the highest, the variation in their length being an inverse index of their position on the stem. This is true of the supernumerary needles of *P. Strobus*, shown in fig. 4, though their relative postions are not indicated. It is very noticeable in *P. Jeffreyi* that it is the spur with the supernumerary needles that proliferates most freely, though sometimes normal fascicles do also.

In general, the needles of fascicles which have proliferated are irregularly deciduous, remaining attached for a good while usually, and often becoming brown and weathered. One can often detect spurs that have proliferated by these needles. I have seen these needles persisting in the Scotch pine when they had become separated as much as three-quarters of an inch by the expanding base of the branch. This forces on one's attention the thoroughness with which the secondary as well as the primary meristems of these fascicles have been revived, the pines in this respect showing complete agreement with the well known condition in the other genera of fascicle-leaved conifers, where, however, normal proliferation is much more abundant. It is significant that normal proliferation in the pines occurs in the branch region of the stem and from fascicles with extra needles or in association with such fascicles.

Only in the seedling have I ever observed that the branch arising normally from a spur bears primary leaves. After injury, however, this is of quite frequent occurrence, especially on young plants. The branch coming from the spur in fig. 10 of *P. excelsa*

[3] Though I did not see these in the young condition, I should infer that they were then green.

has very long green bracts near its base and shows the gradation between fascicled and primordial leaves, to which reference has already been made. I have also found green bracts on the branches from spurs of *P. excelsa*, *P. halepensis*, *P. Jeffreyi*, *P. Laricio*, *P. Pinaster*, *P. Pinea*, *P. Thunbergii*, *P. tuberculata*. These are especially large in the *P. Thunbergii*. I have also observed ordinary proliferation due to wounding in *P. resinosa*, *P. silvestris*, and *P. Strobus*. In most cases these were young trees about 10–15 feet high. In the case of *P. Laricio*, *P. Laricio* var. *austriaca*, *P. resinosa*, *P. silvestris*, and *P. Strobus*, the trees were mature.

In fig. 12 two proliferating bifoliar spurs from an adult Scotch pine are shown. It will be noticed that they are the two uppermost spurs (cf. DICKSON'S observations cited above), and that the injury was done to the apex of the shoot of the year when the little spurs were just developing, not more than one-half an inch in length (see the one attached to the dead apex of the main axis). This is a feature which is usual in other species as well. When the injury is done to the terminal part of the young developing shoot, I have always found a proliferation of the spurs below the injured part. This never extends to the needles of a previous year, nor have I observed that a spur shoot bud can ever be revived after it has remained dormant over the winter, unless some preliminary growth took place the first year. This feature, however, is being investigated by Mr. FRYER, who is carrying on a series of wound experiments on the pines in order to determine at what season, on what year's growth, etc., the best proliferation can be obtained by wounding. He has not found that in the mature tree the spurs of *P. Strobus*, when a year old, can be induced to develop, though those of the season's growth do so very abundantly if wounded early. His test cases were with twigs which had proliferated last year. He tried to arouse the dormant buds of neighboring fascicles by cutting away all but the lowest and smallest of the proliferated spurs. Only those that had grown the year before showed any signs of doing so this year. It seems probable, then, in this species that when the bud of the spur has lain dormant over the winter it cannot be revived. The leaves in this form are shed in the second year, and whether or not those with more persistent spurs can be

made to proliferate after they have undergone one or several winter resting periods has yet to be determined. According to my own observations, it is much easier to induce a young vigorous tree to proliferate than an old slow-growing one, early wounding of the tip of the bud of the season being most effective.

General statement and conclusions

The lack of definiteness in the number of leaves in a fascicle, and the occurrence of supernumerary needles in the recognized primitive region and after wounding, are evidence of the branch character of the spur of the pines. The normal occurrence of single spirally arranged leaves in the seedling, their appearance at times on the cone-bearing branch, their traumatic revival in many instances in the adult, and the transitions which have been found between them and both scale and fascicled leaf, practically demonstrate that ancestrally the leaves of the pines were spirally arranged on ordinary branches, and that the spur is derived from this condition. Its normal proliferation in the seedling and young plant into an ordinary branch with both primordial and fascicled leaves and the traumatic revival of this condition in the mature tree place this conclusion beyond reasonable doubt. In all these features the pines differ from the other spur shoot-bearing conifers only in degree, in conformity with their more specialized condition. If in the one case the spur is a branch, it certainly is in the other. The pine spur shoot, moreover, is wholly vegetative, while in the other forms it is less specialized and combines both the vegetative and the reproductive functions, as is the case in *Ginkgo*, the most primitive of our living spur shoot-bearing forms.

When one comes to compare the conditions in the living pines with their fossil progenitors, several important points develop, which bear out the branch character of the spur. FONTAINE (9) has described several species of pines from the Potomac or Younger Mesozoic, having had to modify HEER's genus *Leptostrobus* slightly for their reception. These remarkable pines had needle-shaped leaves "scattered on the larger or principal stems and grouped in bundles on the ends of short twigs" (p. 227). Some of the fascicles from FONTAINE's work are reproduced in text fig. 2. They bore

more needles than any pine of today does normally, but in this feature and in the fact that they have considerable axis supporting them they remind one of such fascicles as those of *P. excelsa* (fig. 3), which were produced after bud injury. The fascicles of the fossil form, too, are described as terminal as well as lateral, and must have grown out into branches and the main axis, just as has sometimes been observed in the living pines. The lack of differentiation, too, between the primordial and fascicled leaves and the persistence of the former on old branches afford a full explanation of the transitions which have been found between these leaves in the living pines and also of the occasional "revival" of primordial leaves on old trees. In fact, no better "generalized type" could be desired for the ancestors of the pines than FONTAINE has described. Two other fossil forms have also significant features. In *Prepinus* of the Cretaceous, whose discovery we owe to JEFFREY (**14**), the spur shoot has 20 or more leaves. These leaves are not cyclic, but are spirally arranged, and are stated to be subject to considerable variation in number. This spur shoot is nothing more nor less than a small branch with closely set leaves, very similar to the condition described in the seedling of certain pines and in the adult after injury. This spur is apparently deciduous, however, but JEFFREY (**15**) has described one from the Triassic (*Woodworthia*) with very persistent spur shoot, remaining 50 years or more attached.[3]

FIG. 2.—*Leptostrobus longifolius:* from FONTAINE (**9**, *pl. 102*); reduced one-half.

[3] It is recognized that JEFFREY considered this form a pine specializing in the direction of the araucarians and not as an ancestor of the pines and their allies. Since, however, it has been recently shown that no authentic abietinean forms have been described in the strata prior to it (see GOTHAN **10** and THOMSON AND ALLIN **28**), this form must stand as the ancestor of the pines and their allies until some other fascicle-leaved conifer displaces it.

This is certainly a very branchlike feature, and it is noteworthy that it occurs in the most ancient spur shoot-bearing conifer on record.

The paleontological evidence afforded by the fossil pines supplements that from the living forms, and makes the case for the specialized character of the spur shoot of the pines practically complete. The spur then, as it stands today, is only a specialized branch which is of limited (primary and secondary) growth and bears a limited number of specialized and cyclically arranged leaves; whereas its progenitor, judging from the adult living and fossil forms and from the seedling and traumatic phenomena above described, was an ordinary branch. If such is the case, the genus *Pinus* is a specialized one in respect to its fascicled foliage, and the spur shoot of the pines cannot be the indication of primitiveness which JEFFREY'S statement, quoted in the introductory paragraph, would lead us to expect. According to it, the fascicled condition of the leaves is "a primitive attribute of the coniferous stock." This condition, he considers, has been retained in the cone of all, but "in the vegetative parts of only the very ancient genus *Pinus*." It is not apparent why *Pinus* is singled out for this distinction and not some of the other spur shoot-bearing conifers, or *Sciadopitys* whose cladode is recognized by all adherents to the "brachyblast" theory of the cone structure as the closest approximation in the vegetative parts to the condition in the cone scale. Moreover, JEFFREY, in stating the arguments in support of his view, puts much emphasis on the homology of the cone structure of the living and cordaitean forms (**13**, p. 23). The latter, he, in common with many other anatomists, regards as the ancestors of the conifers. If JEFFREY'S inference that fascicled leaves are ancestral for the conifers because of the brachyblast structure of the cone, be applied to the cordaitean forms the logical conclusion is that they must have had their leaves in fascicles. Of this there is not a vestige of evidence. All that the "brachyblast" theory postulates in this regard is the power of branching, a feature which is common to both Cordaitales and Coniferales. If, moreover, the spur is "a primitive attribute of the coniferous stock," we should expect some indication of this in the primitive regions of the non-fascicled conifers; in their seedling, on their fruiting branches, as a result of

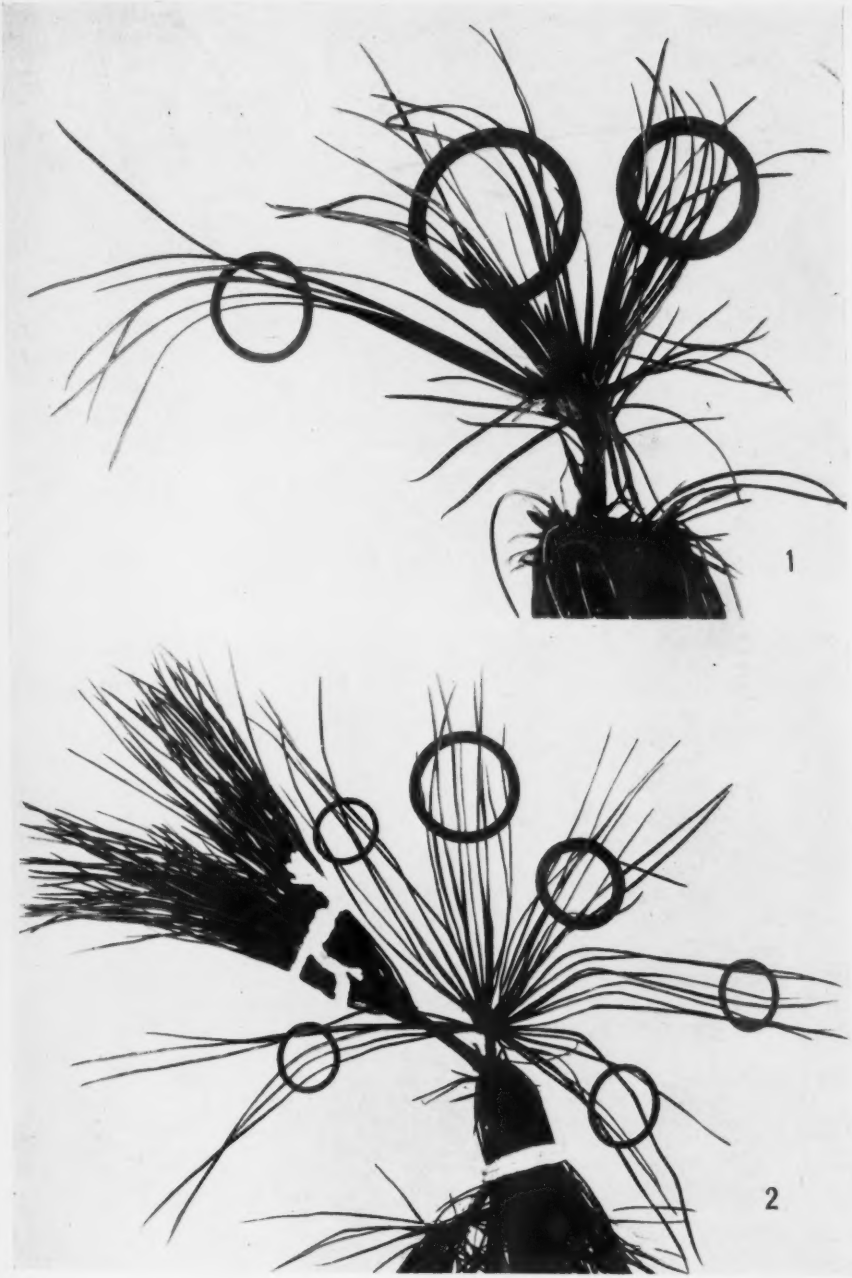
wounding, etc. There is no more evidence of this than of fascicled foliage in the cordaitean forms.

In addition to those whose assistance I have already acknowledged in the body of this article, I am indebted to the directors of the following botanic gardens for the privilege of studying and securing much of the material for this article: the Royal Botanic Gardens, Edinburgh; Der Königliche Botanische Garten, Berlin; Jardin Botanique de l'État, Brussels; the University Garden, Cambridge; and the Royal Botanic Gardens, Kew. By the courtesy of Mr. L. A. BOODLE, I was enabled to photograph several of the specimens in the Jodrell Laboratory. Most of the seedling material was grown in the University Garden here.

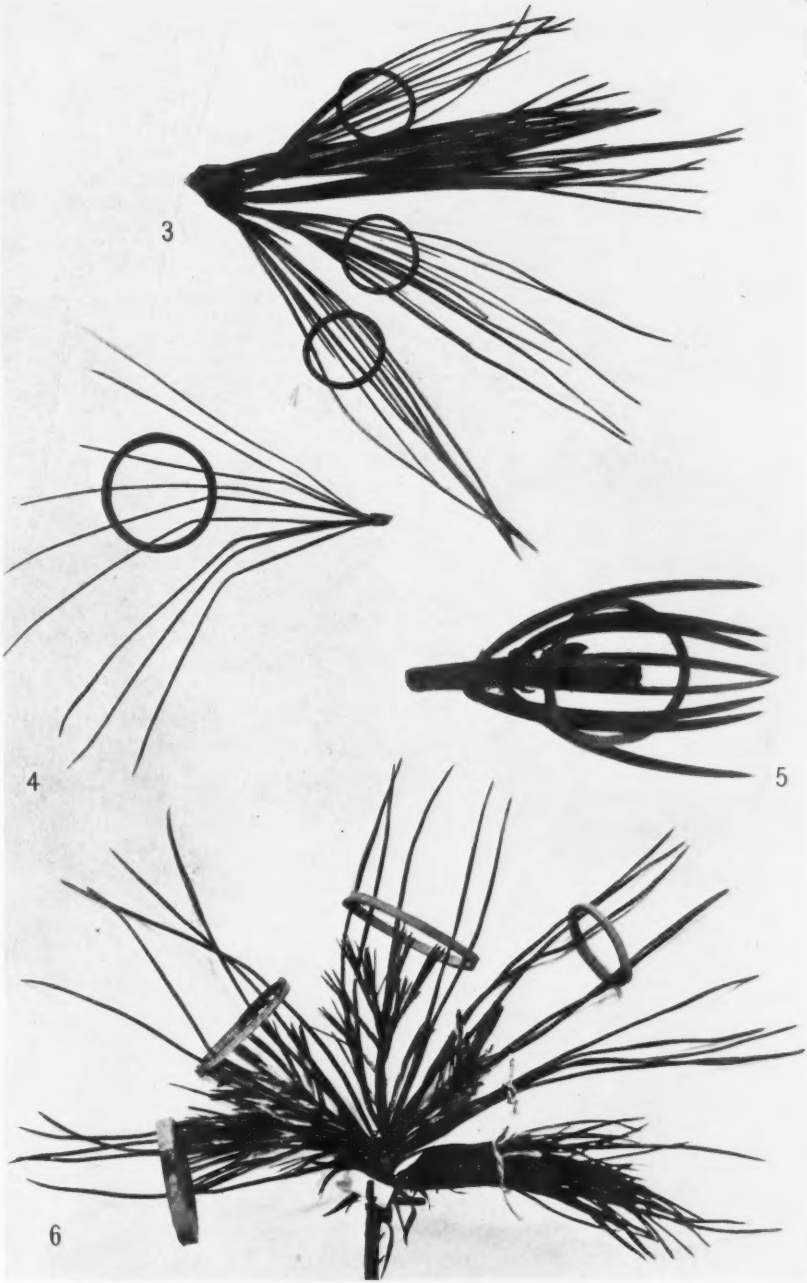
UNIVERSITY OF TORONTO

LITERATURE CITED

1. BORTHWICK, A. W., On the development of quadrifoliar spurs in *Pinus Laricio* Poir. Trans. and Proc. Bot. Soc. Edinburgh **21**:150–153. 1899.
2. ———, On interfoliar buds in pines. *Ibid.* 154–158.
3. BRITTON, N. L., North American Trees. New York. 1908.
4. COOLEY, GRACE E., Ecological notes on the trees of the Botanical Gardens at Naples. BOT. GAZ. **38**:435–445. 1904.
5. COULTER and CHAMBERLAIN, Morphology of gymnosperms. Chicago. 1910.
6. DICKSON, A., On the development of bifoliar spurs into ordinary buds in *Pinus silvestris*. Trans. and Proc. Bot. Soc. Edinburgh **16**:258–261. 1885.
7. ELWES, H. J., and HENRY, A., The trees of Great Britain and Ireland. Edinburgh. 1910.
8. ENGELMANN, G., Revision of the genus *Pinus*. Trans. Acad. Sci. St. Louis **4**:161–190. 1880.
9. FONTAINE, W. M., The Potomac or younger Mesozoic flora. U.S. Geol. Survey **15**:1889.
10. GOTHAN, W., Die fossilen Holzreste von Spitzbergen. Kungl. Svensk. Vetensk. Akad. Handl. **45**: no. 8. 1910.
11. HEMPEL und WILHELM, Die Bäume und Sträucher des Waldes. Wien. 1899.
12. HOCHSTETTER, W., Die sogenannten *Retinispora* Arten der Garten. Gartenflora von E. REGEL. pp. 362–367. 1880.
13. JEFFREY, E. C., The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**:1–37. 1905.

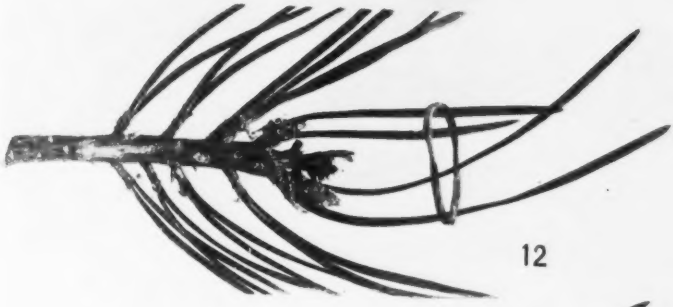


THOMSON on the SPUR SHOOT



THOMSON on the SPUR SHOOT

THOMSON on the SPUR SHOOT



THOMSON on the SPUR SHOOT

14. JEFFREY, E. C., On the structure of the leaf in the Cretaceous pines. Ann. Botany **22**:207–220. 1908.
15. ———, A new araucarian genus from the Triassic. Proc. Boston Soc. Nat. Hist. **34**:325–332. 1910.
16. KRONFELD, M., Bemerkungen über Coniferen. Bot. Centralbl. **37**:65–70. 1889.
17. LLOYD, F. E., On hypertrophied scale leaves in *Pinus ponderosa*. Annals N.Y. Acad. Sci. **11**:45–54. 1898.
18. ———, An unusual pine. Jour. N.Y. Bot. Gard. **12**: no. 137. 1911.
19. MASTERS, M. T., Review of some points in the comparative morphology, anatomy, and life history of the Coniferae. Jour. Linn. Soc. Bot. **27**:226–332. 1891.
20. ———, *Pinus monophylla*. Ann. Botany **11**:124–126. 1897.
21. ———, A general view of the genus *Pinus*. Jour. Linn. Soc. Bot. **35**:560–659. 1904.
22. MEEHAN, T., *Pinus edulis* and *P. monophylla*. Bull. Torr. Bot. Club **12**:81–82. 1885.
23. PHILLIPS, F. J., Two sprouting conifers of the Southwest. BOT. GAZ. **51**:385–390. 1911.
24. SARGENT, C. S., The silva of North America. Vol. XI. Boston. 1897.
25. SHAW, G. R., Characters of *Pinus:* the lateral cone. BOT. GAZ. **43**:205–209. 1907.
26. ———, The pines of Mexico. Publ. Arnold Arboretum, no. 1. Boston. 1909.
27. THOMSON, R. B., On the comparative anatomy and affinities of the Araucarineae. Phil. Trans. Roy. Soc. London B **204**:1–50. 1913.
28. THOMSON, R. B., and ALLIN, A. E., Do the Abietineae extend to the Carboniferous? BOT. GAZ. **53**:331–338. 1912.

EXPLANATION OF PLATES XX–XXIII

FIG. 1.—*Pinus Strobus*, 3 years old.
FIG. 2.—*Pinus Strobus*, 4 years old.
FIG. 3.—*Pinus excelsa*.
FIG. 4.—*Pinus Strobus*.
FIG. 5.—*Pinus monophylla*.
FIG. 6.—*Pinus Strobus*, 3 years old.
FIG. 7.—*Pinus virginiana*.
FIG. 8.—*Pinus Strobus*.
FIG. 9.—*Pinus monophylla*.
FIG. 10.—*Pinus excelsa*.
FIG. 11.—*Pinus Strobus*, 3 years old.
FIG. 12.—*Pinus silvestris*.
FIG. 13.—*Pinus Jeffreyi*.

A PHYSIOLOGICAL STUDY OF THE GERMINATION OF AVENA FATUA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 185

W. M. ATWOOD

(WITH THIRTEEN FIGURES)

I. Introductory

The apparent inability of many seeds to germinate for some time subsequent to harvest has been the object of study both in Europe and in America. The vitalistic viewpoint, which early ascribed such phenomena to the inherent properties of protoplasm, obscured the whole situation. Such germinative delays were found capable of modification by external influences which were said to exert a stimulus on the seed. The later physiological studies have attempted to uncover the nature of the modifications in function which the so-called stimuli bring about.

Many seeds with low germinative power after harvest acquire increased viability in succeeding weeks or months, during a period which has been termed the after-ripening or germ-ripening period. The changes taking place during this period have been found, in general, due to alterations in the structures inclosing the seed, or to modifications in the inclosed members themselves. The term after-ripening has been limited to changes of the latter type (**22**), but in this paper will be used to cover all changes in the seed subsequent to harvest, as a result of which greater germination percentages may be obtained.

The most extensive investigations of germination characters among the Gramineae have probably centered on barley, an early and prompt germination of which is much sought in the malting industries. In agriculture much trouble is occasioned in the small grain regions by the persistence of the wild oat, *Avena fatua* L., and by the difficulty with which it is eliminated. As a cattle food it is undesirable because of the long and twisted awns, and also because of its lightness, averaging about 12–18 pounds per bushel. Laboratory and field tests have shown the seed to germinate very

poorly and unevenly after harvest, and later to increase in viability during succeeding weeks. In the work here described, an attempt has been made to determine the factor or factors restricting the germination of the wild oat, and to investigate the nature of the after-ripening changes taking place in the seed subsequent to harvesting.

II. Historical

1. GERMINATION STUDIES OF THE GRAMINEAE.—It is supposed that the common cultivated oat, *Avena sativa*, has been derived from *A. fatua*. TRABUT (**64**) holds that *A. sterilis* and *A. fatua* have given rise to two series of cultivated oats: *A. sterilis* to those of the Mediterranean region, and *A. fatua* to those of Central Europe. Instances are reported for *A. sativa* of what are thought to be reversions toward the parent stock (**52, 67**). The wild oat is specially abundant in the Pacific Coast region, where four varieties have been reported (**20**): *A. fatua*, the true wild oat; *A. fatua glabrescens*, the bastard oat; *A. barbata*, the slender oat; and *A. sterilis*, the fly oat. The wild oat has been found as far east as Illinois, but is not troublesome east of the Mississippi River. It is especially abundant in the northern small grain belt. Recently CRIDDLE (**16**) has been investigating the false wild oats of Canada, which he believes represent some form of deviation from type which affects the seed coat only and leaves the seed unaltered. By the word "type" reference is made to the normal tame oats from which the false wild oats are supposed to have been derived. Yet he finds one of the most conclusive evidences, as to its distinction from *A. fatua* proper, in the greater ease with which the false wild oat may be germinated. These false wild oats resemble certain tame varieties, and may be due to crossing with *A. fatua*, although much uncertainty has been expressed as to the common occurrence of cross-pollination between *A. fatua* and *A. sativa* (**67**). In 1900 KINZEL (**42**) called attention to the progressive rise in germination percentage of *A. sativa* in the months subsequent to harvest. ATTERBERG (**3**), in his studies of the after-ripening of grain at the Swedish station, finds he can notably raise the after-ripening rate by drying the seed at higher temperatures. Wounding has also

hastened the germination of barley. He believes the temperature at which small grain will germinate is a measure of the degree of after-ripening. Thus, if seed will not grow at 13–15° C., preliminary drying is necessary; while if the seeds are capable of growing at 30° the process of after-ripening is complete. He believes the after-ripening is but the completion of the ripening processes in seeds which have been harvested so late that normal ripening has not occurred. ZADE (**67**) notes the delay of germination of freshly harvested *A. fatua*, and that it may be influenced by various external factors, but does not attempt to explain the effects of these various factors. He finds the delay is much shorter in seed kept in dry air of the laboratory than in that lying in the field, due as he believes to the difference in temperature. JANSON (**38**) notes two degrees of maturity in barley and oats, which he calls "yellow-ripeness" and "dead-ripeness." The ripening of oats up to the yellow stage results in a larger increase in the protein stuffs. After yellow-ripeness one-third of the total increment occurs, and is only nitrogen-free stuffs. He thus believes too early cutting results in considerable carbohydrate loss to oats, for the effect of after-ripening extends only to the early stages of normal ripening, which concerns proteins chiefly. KIESSLING (**41**) recognizes the beneficial effects of drying upon germination, but believes that germ-ripening or after-ripening is a process in general independent of seed-moisture content. He reports an elaborate series of tests under various conditions modifying germination, and concludes as regards oats that germ-ripening is a characteristic varying with the strain tried. He discredits explanations of after-ripening or germinative variations which are based on seed coat exclusions of water or gases, or on enzymatic alterations as so far set forth; yet believes that in some way enzymes are associated with germ-ripening.

2. GENERAL GERMINATION STUDIES.—No attempt will be made to cite all the recent literature on the general field of germination. However, a few instances may be cited to show that such problems have been approached from at least three different angles: (1) studies of germination factors external to the embryo; (2) factors associated with chemical or physical alterations of members within

the seed coat; (3) enzyme studies. In the studies of factors external to the embryo, CROCKER (17, 18) found the seed coat obstructs in various cases the entry of oxygen or water. A. J. BROWN in a study of *Hordeum* (9, 10) found that non-living structures inclosing the embryo have the power of excluding various salts and acids in solution. This work was extended by SCHRÖDER (59) for wheat; while REICHARD (57) would explain this peculiarity for barley by saying that there is a causal relation between the solubility of the tannins in the seed coat by various agents and the ability of these agents to penetrate the seed. Wounding and its effect on germination has been noted by various investigators (12, 17, 30, 31, 39, 41, 65). The germination rate of *A. fatua* has been increased by alternations of moisture and dryness (51). Other factors concerned with germination of seeds as so far studied are drying (3, 41, 67), freezing and thawing (23, 53, 54), effect of burying in soil (4, 21), subjection to various gases during storage and germination (41), effects of light (25–28, 35, 36, 43–47), of treatment in hot water (5, 41), and in dilute acids (22, 24).

Chemical and physical studies have been made of alterations in the endosperm or embryo of various seeds. H. T. BROWN (13) believes that in after-ripening of barley cytase, acting on the middle lamellae of the cell walls, changes the earlier glazed condition of the endosperm to a mealy structure, following which better germination is possible. JOHANNSEN (39) correlates after-ripening with fluctuations in the sugars and amide nitrogen stuffs, while ZALESKI (68) has followed the ripening process of peas and found protein increases at the expense of amino acids, amides, and organic bases. KIESSLING cites work (41) emphasizing the relation between the protein content in grasses and the speed of germination.

The third type of germination studies, dealing with enzymatic relations, includes a large number of researches. BROWN and MORRIS (12) in their study of *Hordeum* believe that the development of amylo-hydrolytic enzymes is located in the epithelial cells of the scutellum, and think the zymogens of the resting seed on germination are activated by the development of acidity. In this view as to the function of acidity in relation to enzymes, they follow the ideas of GREEN (29). In 1892 HOTTER (37) expressed

the view that the diastatic content of wheat increased in the resting seed, coming to its full possibilities at the time of germination. This after-ripening could be hastened by warming and air-drying of the seeds. DETMER (**19**) showed that oxygen entry is necessary for the formation of diastase. LEHMANN and OTTENWÄLDER (**49**) would explain the forcing of germination by various factors as due to hydrolysis of the proteins. These views are based on experiments in which temperature variations were employed, nutrient solutions were used, and also splitting products of the proteins as asparagin. ABDERHALDEN and DAMMHAHN (**1**) believe that germinated and ungerminated seeds vary in the presence or absence of peptolytic ferments, while APPLEMAN (**2**) for the potato and Miss ECKERSON (**22**) for *Crataegus* trace enzymatic alterations in after-ripening. In the latter case there are also found alterations in the acidity and water-holding power of the embryo. Recently, PUGLIESE (**55**) has investigated the autolysis of oat seeds which had not germinated, and concludes that ungerminated ones may be distinguished from the germinated ones by the presence or absence of amidases or enzymes caring for the end products of the proteolytic digestion. If such enzymatic differences exist between seeds which have been germinated and those which have not, there is quite possibly a very worthy field for investigation in the enzymatic differences between the freshly harvested and the after-ripened seeds, although these differences may not be associated with the problem of dormancy.

It is evident that the conflicts of opinion and the apparent conflicts of fact must be harmonized, if at all, only in the light of careful quantitative determinations of the various factors involved, under standard conditions, and with uniformity of experimental material.

III. Experimental

The work described in this paper has been carried on with seeds of *Avena fatua* received from the Dominion Experimental Farm at Indian Head, Saskatchewan, of the crops of 1910, 1911, and 1912. Parallel tests have been made with seed from Grand Forks, North Dakota, from Brandon, Manitoba, and with seed raised in Chicago

in the summers of 1912 and 1913.[1] Comparisons have been made in many cases with the varieties of *A. sativa* known as Lincoln, Swedish select, Kherson, and White Tartar.

1. GERMINATION TESTS.—Germinative tests made through a considerable period showed for the wild oat seed tested the same progressive increase in percentage of germination which has been noted by other investigators for various grasses. From many tests made those given in table I are typical, A and B representing two varieties.[2]

TABLE I

WILD OATS HARVEST OF 1911

TESTED	SHELL COATS ON		SHELL COATS OFF		IN SOIL	
	A	B	A	B	A	B
December	0.5	4.3	48.0	35	.....	.....
January	.....	.....	70.9	.....	64	.....
March	29.0	.....	90.0	.....	94	.....
April	.....	52.0	.....	84	.....	77
June	60.0	26.0	81.0	86	.....	.....
August	37.0	30.0	93.9	79	96	63

Germination tests were made in Petri dishes on moist absorbent cotton at a temperature of about 20° C. Soil tests were made in the greenhouse, even watering being accomplished by the porous clay cup method (**34**). As pointed out by ZADE, the germination is much better with the shell coats removed. However, there is a rise in germination rate apparent through the after-ripening period by seeds from which they have been removed. The peculiarities of germination are thus not to be attributed to low vitality of the seed used, nor to exclusion effects of the shell coats.

In meeting the problem of after-ripening, it is evident that changes must take place during this period either in the structures inclosing the embryo or in the inclosed members themselves. Tests were undertaken designed to furnish data on this situation. The seed coat of *Avena fatua* is formed by the combined cell layer

[1] For these samples I am indebted to Dr. M. A. BRANNON of Grand Forks, Mr. ANGUS MACKAY of Indian Head, and the Dominion Farm at Brandon.

[2] The term "shell coat" is used in this paper to include the palea and lemma inclosing the seed as opposed to the true seed coat.

remnants of the original ovary wall, the integuments, and the epidermis of the nucellus (**14, 32**). This coat cannot be removed from the endosperm and embryo without injury, and thus attention must be called to the difficulties which are immediately encountered in studying the coat effects of the oat. To know absolutely what the coat effects are is impossible; for to break the coat involves dangers of "wound effects," or of infection; while if the seeds are subjected to fluids or gases, it cannot be said with certainty that any results obtained are due primarily to the external

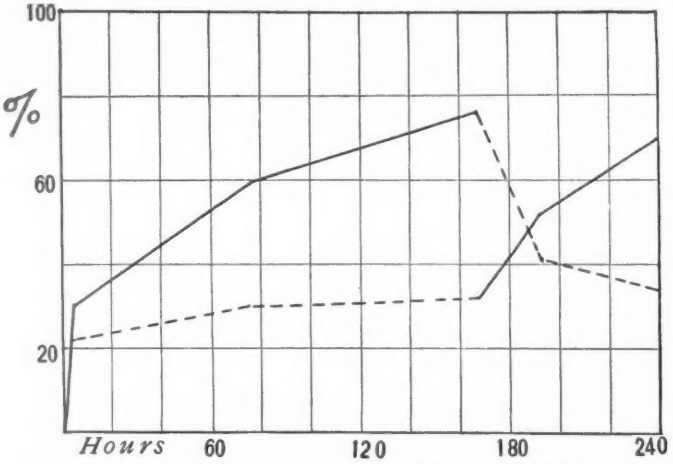


FIG. 1.—Water intake, showing semipermeability of the wild oat; increments in percentage of air dry weight; in water, solid line; in gram-molecular sodium chloride solution, broken line.

agents used, as questions of their actual entry to the embryo arise, and also the question as to what exact physiological function is set in action by such agents, even if they are successful in forcing germination. These difficulties are of course obviated in experimentation with seeds which, like *Xanthium* (**60**), permit of an easy removal of the seed coat. However, in a study of *Avena* it is necessary to gather as much data as possible from a variety of external factors, and, recognizing the uncertainty to which any one line of inquiry alone leads, to judge the situation from the combined results.

2. WATER INTAKE.—BROWN'S work on the semipermeability of *Hordeum* led to like tests of *A. fatua*. Distilled water and gram-molecular solutions of sodium chloride display on test a rather close approximation to perfect semipermeability (fig. 1). Later work by SHULL (**61**) in this laboratory shows that the power of excluding various salts in solution by non-living membranes is a rather common property of seed coats. It was thought possible that there might be some correlation between this behavior of *Avena* and gaseous or water exclusions in unafter-ripened seeds.

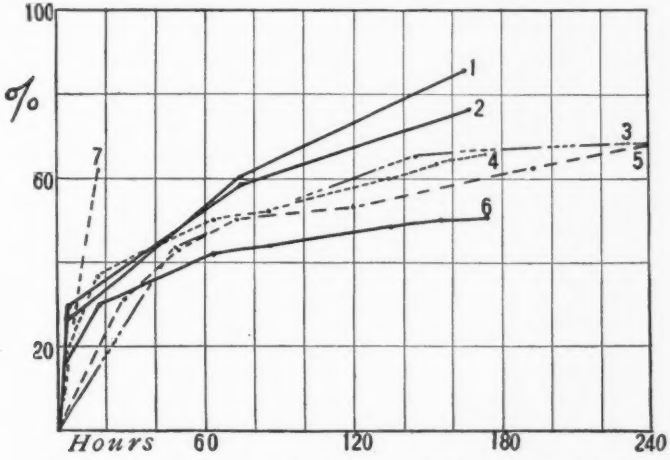


FIG. 2.—Comparative water intake among the Gramineae and in *Xanthium;* increments in percentage of air dry weight; curves: *1*, wild oats 1911; *2*, wild oats 1910; *3*, barley; *4*, *Avena sativa; 5*, wheat; *6*, wild oats 1911; *7*, *Xanthium*.

Tests were thus made of the rate of water intake for seed of different crops and for *A. sativa*, the shell coats being removed in all cases (fig. 2). Comparing the data derived with figures given by SCHRÖDER for *Triticum* and by A. J. BROWN for *Hordeum*, there is seen to be a general similarity in the rate and total water intake for these grasses. Although much slower than the water intake of some other seeds, as for instance *Xanthium* (**17**), there does not seem to be any ground for saying that water exclusion in the case of *A. fatua* can explain its peculiarities of germination in the light of the general behavior of *A. sativa*, *Triticum*, and *Hordeum*.

3. WOUNDING.—Various attempts were then made to see if the slowness of germination soon after harvest could be influenced by other external factors. Tests of light and darkness did not seem to indicate for the wild oat the importance ascribed to these factors by German investigators for other seeds. Using a sterilized needle and pricking the true seed coat of seeds from which the shell coats had been removed tended to raise the germination percentage as pointed out by several other workers. The results given in table II were typical.

TABLE II

No. tested	Month	Per cent germination	
		Pricked	Check
100	December 1911	100	35
100	December 1912	97	48

As regards the relation of seed wounds and water intake, COUPIN (15) has shown that wounds increase the speed of intake, but have no influence on the maximum absorbing power. In order to accomplish the same result of breaking the seed coat without so much danger of infection, the method was adopted of searing the seed near the embryo with a red hot needle. Similar increases in germinative percentage were again noticed. To determine whether the modified behavior of seared seeds could be attributed to "wound effects" of a temporary character, dry seeds were seared, and after a month compared with other seeds previously soaked in water for 24 hours in the ice chest and then seared just before placing in the germinator. No marked difference could be noted in the two lots. Typical results of searing the seeds of *A. fatua* are shown in table III.

TABLE III

Time	No. seeds	Per cent germination	
		Seared	Check
February 1912	100	95	74
March 1912	100	100	90
December 1912	100	99	52
December 1912	100	95	64
January 1913	100	100	67
January 1913	100	98	68

It will be noticed that the difference between the checks and the treated seeds becomes increasingly less conspicuous with the passage of time after harvest, that is, as after-ripening progresses. Tests were made of fresh seed hardly yet "out of the milk," which tend to show that the seed is then neither lacking in vitality nor under the necessity of a long process of drying to secure "necessary protoplasmic alterations." One test (table IV) will show the tendency.

TABLE IV

No. tested	Period	Per cent germination	Then	Additional percentage	Total percentage
50	4 days	28	Seared 3 days.....	70	98
50	4 "	36	In 40 per cent O_2 3 days.....	34	70

In this connection it is interesting to note that ZADE found that seed harvested unripe yielded a higher percentage of germination than seed harvested after ripening. It has been suggested-(**49**) that seeds sometimes grow better just before ripening due to the presence of enzymes and protein-splitting products which decrease in amount with ripening as proteins are stored. However, if coat restrictions be concerned in the delay of after-ripening, it is possible that ripening tends to increase the impermeability of this coat. It was also found that improved germination could be secured by complete separation of the embryo from the endosperm. Other workers have successfully grown seeds thus mutilated (**30, 65**). The results secured with *A. fatua* may be illustrated by the instances given in table V.

TABLE V

Time	No. tested	Embryos alone per cent	Check per cent
December 1911.....	100	87	35
December 1912.....	100	87	48

4. RESPIRATORY RATIO.—In considering the effect of breaking the seed coat and its relationship to germination, the question arose as to whether if the seed coat acted as a restriction to oxygen entry, it might not be possible that after-ripening consists in a developing ability of the seed for anaerobic respiration. This was found not

to be the case. The results obtained, however, were interesting in another way. In making these tests, 25 seeds with like control were soaked over night in distilled water in the ice chest, and then placed in inverted test tubes over mercury and kept in the dark at a quite evenly registered temperature of about 21° C. Seeds were allowed to remain about four hours, a period during which the oxygen content of the tube was found not to fall below 16 per cent. At the end of the period the gas was drawn off and analyzed for carbon dioxide and oxygen with a Bonnier and Mangin gas apparatus in the customary manner. From this data the respiratory ratio $\frac{CO_2}{O_2}$ was computed. Tests were made for the seeds intact, seared, and intact but in 93 per cent oxygen. Anaerobic respiration apparently did not increase in the three months (January to March 1913) during which these tests were being carried on. The point to these results, however, may be noted on taking the average of many determinations made under the three conditions given in table VI.

TABLE VI

	Ratio average
Seeds intact in pure air	0.800
Seeds seared	0.649
Seeds in 93 per cent oxygen	0.557

It is interesting to note the decrease of the ratio as the seeds are seared, and an even greater decrease as they are subjected to increased oxygen concentrations. The results do not seem to be out of harmony with the conception of the seed coat acting as a restriction to oxygen entry.

5. GERMINATIVE TESTS UNDER VARYING CONDITIONS OF OXYGEN.—If the coats should thus tend to exclude oxygen, we might suppose that seared seeds would be able to germinate in an atmosphere of reduced oxygen content as well as intact seeds in air; while intact seeds, it might be supposed, would be benefited in germination percentage if placed in an atmosphere of increased oxygen content. To test out these hypotheses, the seeds were placed on moist absorbent cotton in dishes on tripods, and covered by an

inverted battery jar set in a water seal so as to leave the seeds 2.25 liters of gas, which was introduced by displacement. All was

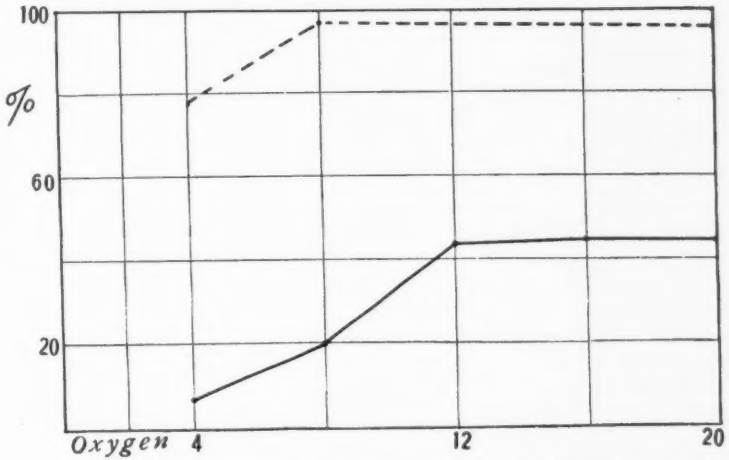


FIG. 3.—Percentage of germination of wild oats in reduced oxygen concentrations; intact seeds, solid line; seared seeds, broken line.

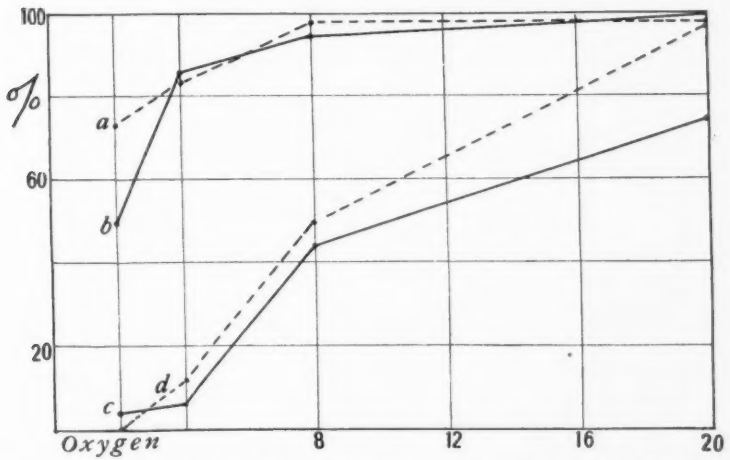


FIG. 4.—Comparison of germination percentages of tame and wild oats in reduced oxygen concentrations; intact seed, solid line; seared seed, broken line; *Avena sativa*, curves *a* and *b*; *Avena fatua*, *c* and *d*.

placed in a dark room at about 20° C. For oxygen content less than the approximate 20 per cent of air, hydrogen was used as dilutant; while for increased oxygen content, the gas was added

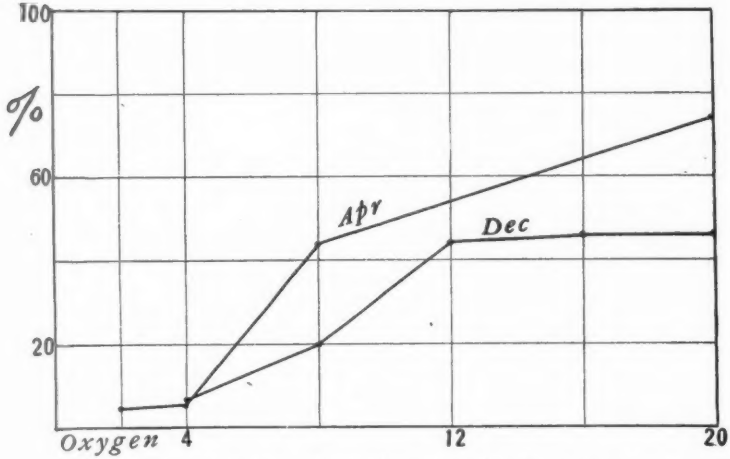


FIG. 5.—Comparison of germination percentages of wild oats in reduced oxygen concentrations in autumn and spring.

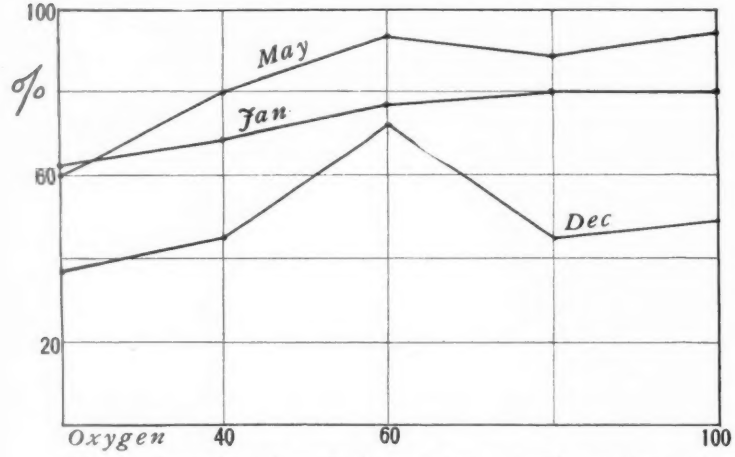


FIG. 6.—Comparison of germination percentages of wild oats through after-ripening period in increased concentrations of oxygen.

directly. The gas used was generated electrolytically by the American Oxhydric Company of Milwaukee, and showed high percentage of purity on analysis. Considering the air check as 20 per cent oxygen, tests were made at the further percentages of 2, 4, 8, 16, 40, 60, 80, and approximately pure oxygen. Comparing the effect of reduced oxygen content on the germination of both intact and seared seeds of *A. fatua*, greater ability is noticed for the seared seeds to grow with good percentages in concentrations of one-fifth the normal oxygen during December (fig. 3).

For April and May, if we compare the sound and seared seeds of *A. fatua* and *A. sativa* as shown in fig. 4, it is evident that searing increases the germination of both at all percentages of oxygen, the difference caused by searing being greater for the wild oat. The tame oat shows a high germination rate even in very low concentrations of oxygen. If we follow the intact wild oat through the winter, there is a noticeable rise in the ability of the seed to grow at lowered oxygen concentrations (fig. 5). If, on the other hand, increased concentrations of oxygen be tried upon *A. fatua* through the after-ripening period, there is noticeable a larger percentage of germination with increased oxygen concentrations up to about 60 per cent, beyond which point the seedlings tend to become stunted. The rise in viability from December to May is also noticeable (fig. 6).

6. MEASUREMENTS OF OXYGEN ABSORPTION.—The above results with variations in the oxygen concentration and in the season of the year may indicate either that as the season progresses there is a decrease in the embryo requirements for oxygen necessary to secure germination, or that there are modifications taking place in the seed by which the entry of oxygen may be more easily accomplished. To determine the nature of the rates of absolute oxygen absorption under these varying conditions, and as compared with *A. sativa*, a modification of the eudiometer, as devised by CROCKER, was employed (fig. 7). Seven seeds were used in each chamber. They were weighed to 0.1 mg., and moisture content determined in other seeds from the same lot, from which data the dry weight of the seeds used was computed. Before setting up the apparatus, the seeds were soaked over night in distilled water in the ice chest.

The seeds tested were suspended from platinum baskets at *A*, being laid on moistened neutral asbestos fiber, the non-organic substance being used to prevent drying out during the test, and at the same time to avoid danger of respiratory changes. Under the baskets were placed small vessels, each containing 1 cc. of 4 per cent potassium hydroxide solution to absorb any carbon dioxide evolved during the period. Test tube *D* was filled with mercury and could be raised and lowered to balance the mercury column in *C* with that in the test tube. Tube *C* was 15 cm. long and had a volume of 2 cc., the graduations for which were made so that readings could be made to 0.01 cc. When the rate of oxygen intake from the air was to be measured, the gas in the apparatus was previously displaced for several minutes with a current of air forced through 40 per cent potassium hydroxide solution to remove any traces of carbon dioxide. Other gases tested were passed through the alkali and apparatus in like manner. During the course of taking the readings, the apparatus was submerged in a Freas constant temperature water bath electrically regulated and accurate to about 0°.01 C. The volume of the chambers was so selected that variations in temperature would introduce an error so small as to be negligible with the water bath used. Thus, for the right chamber a variation of 0°.1 C. would result in an error of 0.0056 cc., and for the left chamber of 0.0062 cc. Corrections for barometric and temperature variations were made; hence any rise of the mercury column as shown by the corrected readings indicated absolute absorption of oxygen by the seeds tested. From the basis of the dry weight of the seeds used the rate of oxygen absorption per gram per hour was com-

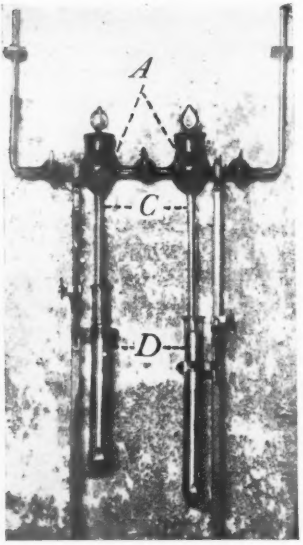


FIG. 7.—Respirometer

puted for the various periods tested. The two chambers served to check all readings. It was found that quite consistent rates were obtained. The rates of oxygen absorption were measured with the bath at the temperature of 21° C.

Before considering the data derived from the respirometer readings, it must be borne in mind that one of the objects sought is to gain a clearer idea of any changes which may occur in the embryo during the after-ripening period. The gas absorption measurements are for the whole seed, of which the embryo forms, by weight, a small part. Hence any variation in the corrected reading for the whole seed might indicate a far greater comparative variation for the embryo. STOWARD (63) has compared the respiration of the separated endosperm and embryo of barley. He finds that per gram of fresh weight, the respiration of the embryo alone is 17 times that of the endosperm, but as the endosperm weighs about 17 times as much as the embryo, these parts probably about halve the respiration of the intact seed. To reason from the respiratory behavior of the separated units to the nature of the respiration of the intact seed seems sufficiently uncertain to justify at least

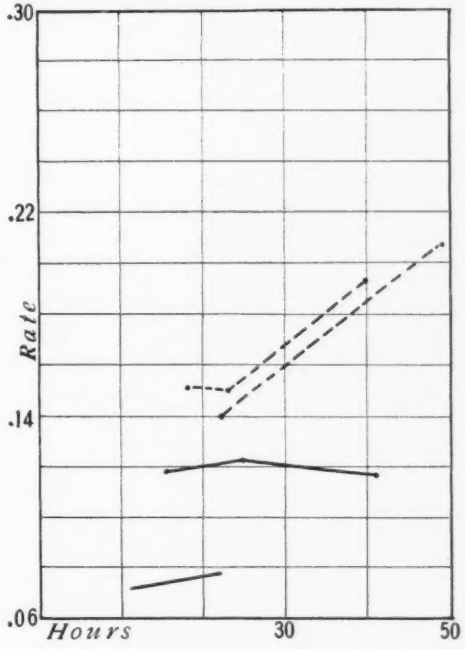


FIG. 8.—Rates of oxygen absorption for wild oats during December and early January in terms of cc. per hour per gm. dry weight; rate for intact seeds, solid line; for seared seeds, broken line.

calling attention to the fact of the combined participation of the embryo and endosperm in the data below.

From a large number of determinations the following will give an idea of the results. Each curve represents the average of the rates derived from both chambers for the periods tested. In fig. 8, curves are shown indicating the absorption rates for intact and seared seeds. These determinations were made during December and early January, when the germination was averaging about 60 per cent for intact seeds. It is evident that the absorption rate is raised noticeably by searing. In most of the curves, a steady tendency is noted for the rate of absorption to rise with the length of the period tested. In many cases the high absorption noted beyond the 25–30 hour periods is associated with the breaking of the seed coats in germination. Earlier increases in rate, however, must not be ascribed to this cause. If now for this same period comparison be made of the absorption rates in the air and in an atmosphere of 93 per cent oxygen, the difference between the two conditions is marked (fig. 9). Further tests in 79 per cent oxygen revealed rates midway between those found for air and for 93 per cent oxygen; while absorption in 7 per cent oxygen

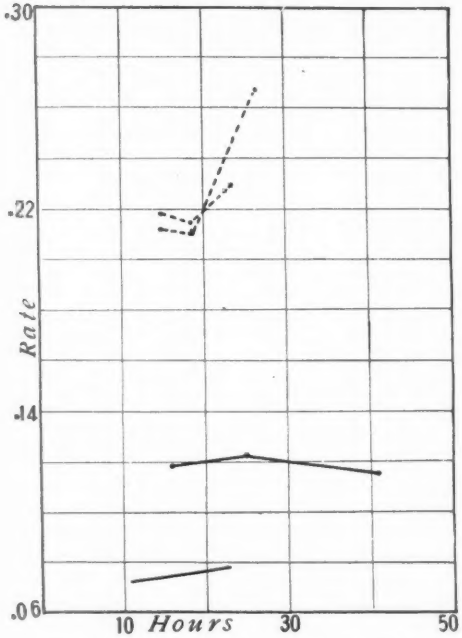


FIG. 9.—Rates of oxygen absorption for wild oats for December and early January in terms of cc. per hour per gm. dry weight; rate for intact seeds, solid line; for seeds tested in 93 per cent oxygen, broken line.

showed much lower rates for the same period than were obtained in air.

Oxygen absorption tests of freshly harvested wild oats were made during July 1913 at temperatures of 16°.2 C. and 26°.2 C. It was thought possible that the failure or success of the VAN'T HOFF temperature law of chemical reaction to hold with the fresh seed might, in connection with the other data, throw some light on the power of the seed coat to exclude oxygen. Summarizing a number of readings, it was found that

$$\frac{\text{the rate at } 26°.2 \text{ C.}}{\text{the rate at } 16°.2 \text{ C.}} = \frac{0.160}{0.067} = 2.38.$$

This is quite what might be expected if the coat offered no restriction to gaseous penetration, and appears at first to conflict with the data derived on this point in other tests. However, we cannot as yet say what effect such a temperature change may exert on the permeability of the coat, which is a non-living structure. It is a well known fact that the solubility of oxygen in water decreases with a rise in temperature. Thus, the absorption at 35° C. is 56.9 per cent of that occurring at 5° C. GASSNER in a recent article (**28**), as reviewed by LEHMANN (**48**), believes that the beneficial results obtained in germination of *Chloris ciliata* through the use of low temperatures may be due to the greater absorption of oxygen at these temperatures. He employed temperatures varying from 5° C. to 34° C. LEPESCHKIN (**50**) and others, however, have pointed out the fact that the permeability of living protoplasm to gases increases with rising temperature. It is thus quite possible that the problem of oxygen absorption by the grasses may be complicated by the opposite influence of high temperature on the solubility of oxygen in the water in the seed, and on the permeability of the seed coat itself. Conclusions on these tests must hence be delayed pending further investigation of the effect of varying temperatures on the permeability of non-living membranes to gases.

As it was noted that in every germination test a large number of seeds laid dormant, yet if forced by searing would promptly germinate, the experiment was tried of testing the oxygen-absorption

rate with seeds selected after lying dormant five days under the usual germinative conditions. The results showed a much lower absorption rate, both in air and in 93 per cent oxygen, than was the case in tests made with unselected seed. Furthermore, the difference between the rates in air and in higher concentrations of oxygen was not so marked. It is realized, of course, that the "selected seed" was not in behavior to be strictly compared with seed treated in the usual manner, as they were subjected to a temperature of 21° C., in the period that germination was attempted before the respirometer test.

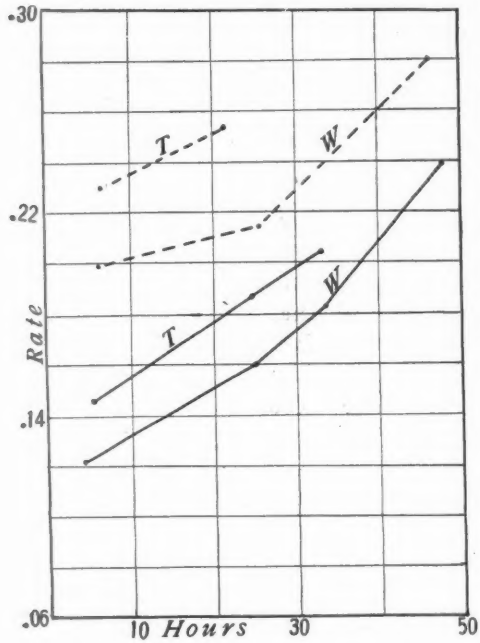


FIG. 10.—Comparative rates of oxygen absorption for tame and wild oats in terms of cc. per hour, per gm. dry weight; *Avena sativa* indicated by *T*, and *Avena fatua* by *W;* rates for intact seeds, solid line; for seared seeds, broken line.

The oxygen absorption seemed to be practically the same for seeds seared dry one month before testing, and those seared after one night of soaking in the ice box, just previous to placing in the respirometer. The similarity in germinative behavior of the seeds treated in these two ways has been noted above. Other workers (6, 58, 62) have studied the influence of wounding on respiration as measured by the resultant carbon dioxide releasal. JUNITZKEY (40) holds that oxygen absorption and carbon dioxide releasal may be phenomena independent of each other. In any case, we are concerned here only with the direct rate of oxygen absorption by the seed as bearing on the problem of germination. For this

reason it is of interest to note that the temporary "wound effects" noted for other tissues with carbon dioxide as a basis of decision, do not hold for the oxygen intake of *Avena fatua*.

As the early germinative delays of *A. sativa* are so much less pronounced than is the case for *A. fatua*, it is of interest to compare the oxygen-absorption rates for the two (fig. 10). The tame oat shows a higher rate throughout. It was impossible to carry out these tests (summarized in fig. 10) until April, when the comparative difference in germinative delay between the tame and the wild oat is much less than in the preceding autumn. This makes it seem probable that when fresh seed may again be obtainable, the differences in rate found above, though quite marked, may be even more conspicuous.

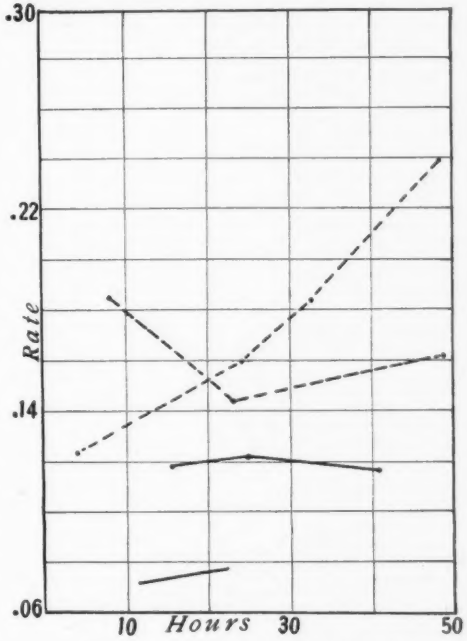


FIG. 11.—Rates of oxygen absorption for intact wild oats before and subsequent to after-ripening in terms of cc. per hour per gm. dry weight; rates in winter, solid line; in spring, broken line.

In figs. 11–13 are shown respectively the effect of after-ripening on the rate of oxygen intake by intact seeds, seared seeds, and seeds run in an atmosphere of over 90 per cent oxygen. The temperatures employed were identical in the 24 tests here summarized. In each case the winter rate is indicated by the unbroken lines, and the spring rate by broken lines. A consistent increase in the rate of oxygen absorption in

higher concentrations is shown. This increase is least noticeable in the case of the high percentage of oxygen tests. It is suggested that if coat restrictions are concerned, and if their effects are overcome by high concentrations of oxygen, the four curves would tend to come together, as is found to be the case.

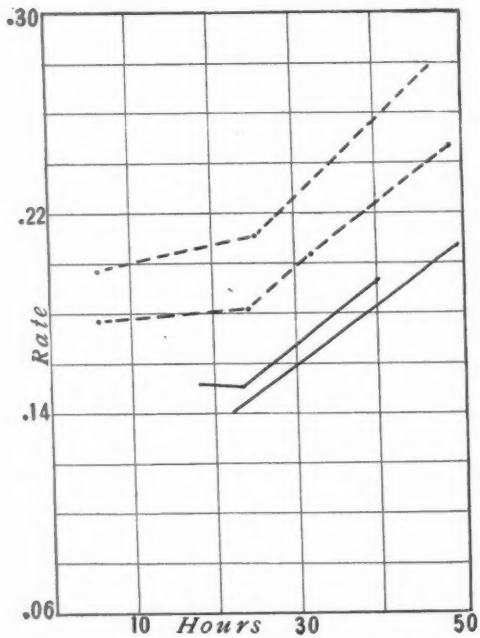


FIG. 12.—Rates of oxygen absorption for seared wild oats before and subsequent to after-ripening in terms of cc. per hour per gm. dry weight; rates in winter, solid line; in spring, broken line.

Summarizing the respiration tests, it would seem that associated with increased germinative rates accompanying after-ripening there is an increased ability of the seed to take up oxygen, providing always that the conditions of germination be the same; and, further, that wounding and subjecting to increased oxygen concentrations actually increases the oxygen intake. Nevertheless, the process of after-ripening may not consist primarily in an increased ability of the embryo to take up oxygen. If the unafter-ripened seeds be freed from limitations to absorption, as was accomplished in the experiments summarized in fig. 12, it is apparent that their oxygen-absorption rate closely approximates that of the seeds which have thoroughly after-ripened. Thus the changes, whether they be seed coat or embryonal, which we ordinarily term after-ripening, and which are exhibited by increased rate of oxygen intake, may be immediately attained by artificially overcoming

the limitations to oxygen entry, if rate of absorption be taken as a basis of judgment.

7. DETERMINATION OF EMBRYO ACIDITY.—Investigation has been begun as to variations in the acidity of the embryo in after-ripening, and comparisons have been made with the embryos of *A. sativa*. To test this condition, the seeds were soaked over night in the ice box, and then subjected to identical germinative conditions for about 18 hours. The embryos were then removed, accurately weighed, carefully ground, and immediately titrated with N/20 alkali in the presence of phenolphthalein. Water content of the embryos was determined on other parallel samples, from which data the dry weight of the titrated embryos could be computed. Figuring then the number of cc. of N/20 alkali necessary to neutralize the acidity of the equivalent of one gram dry weight of the embryos, the results given in table VII were obtained.

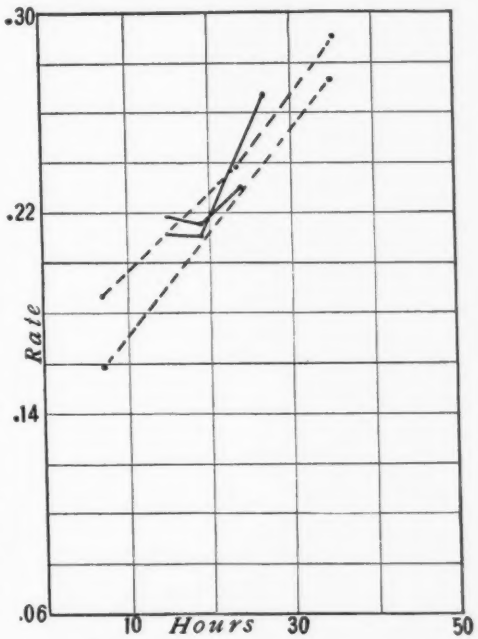


FIG. 13.—Rates of oxygen absorption for wild oats in high concentrations of oxygen before and subsequent to after-ripening in terms of cc. per hour per gm. dry weight; rates in winter, solid line; in spring, broken line.

It will be noticed that the 1912 samples grown at Chicago were tested early and were less acid than corresponding year old samples of both the tame and of the wild. Further, the acidity is less in *A. fatua* seeds one year old than in *A. sativa* just harvested.

Comparing the degree of acidity of the various samples with the moisture contained in the respective embryos, the relations appearing in table VIII are found.

TABLE VII

EMBRYO ACIDITY COMPARISONS OF AVENA FATUA AND A. SATIVA

TESTED AUGUST 1912		N/20 ALKALI FOR 1 GM. DRY WEIGHT
Kind	Season grown	
Tame (Swedish select)	1911	3.70
Tame (Swedish select) tested fresh	1912	2.51
Tame (Kherson)	1911	3.37
Wild (Indian Head)	1911	2.37
Wild (grown Chicago) tested fresh	1912	1.87

It is seen that there is a general tendency for the water-holding power and the acidity to rise contemporaneously. This situation was noted by Miss ECKERSON for *Crataegus*. It is possible that such embryonic changes in *A. fatua* may be causally related to alterations in inclosing structures. Further investigation of the chemistry of the embryo is planned.

TABLE VIII

N/20 alkali to titrate 1 gm. dry weight	Per cent water in embryos
1.87	50.2
2.37	56.0
2.51	54.3
3.37	71.0
3.70	68.3

8. CONCLUSIONS.—The combined results, so far noted, namely, that germination can be increased by various coat-breaking methods; that germination may at all stages be improved by increased oxygen; that when wounded or subjected to increased concentrations of oxygen there is an absolute increase in the rate of oxygen absorption; all seem to point to the conclusion that oxygen supply is for the freshly harvested wild oat the limiting factor to germination, with the probability that coat restrictions to oxygen entry play a rôle. The question still is open as to the nature of the physiological processes for which oxygen is thus essential. GRÜSS (31) believes that in the case of *Phaseolus* the abundant

enzyme content in the cells neighboring a wound occurs as a result of the action of oxygen on the reserve proteins. LEHMANN (49) believes germination stimuli are effective through their influence on protein hydrolysis. The work of Miss ECKERSON and of GREEN suggests the possibility that the development of acidity leads to the liberation of enzymes. What relationship, if any, there may be between acidity, oxygen, enzymes, and germinating power in *A. fatua* is worthy of further investigation.

The character of the changes in the seed of *A. fatua* with after-ripening remains to be discovered.

Oxygen being considered the limiting factor to germination for the freshly harvested seed, it is possible to consider that the embryo in the course of after-ripening either decreases in its demands for oxygen, whereby the seeds become able to grow in gases poor in oxygen; or we may suppose that there is no decrease in oxygen demands, but rather an increased permeability of the coat to oxygen. The fact that after-ripened seeds can grow better than fresh seeds in chambers poor in oxygen, although the former regularly absorb oxygen at a more rapid rate in respiration under normal conditions, together with the results (as shown graphically in fig. 13) that fresh and after-ripened seeds in the presence of high percentages of oxygen absorb at similar rates, seem to favor, but not to prove, the general idea that the coat exclusion to oxygen becomes less complete as the seed after-ripens. What mechanism is released by the greater oxygen supplied either artificially through breaking the coat, or submitting the seed to high percentages of oxygen, or under natural conditions through a slowly developed increase in the coat's permeability to oxygen, is as yet an open question. If further investigation upholds the data given above, showing an increased acidity of the embryo with after-ripening, we must recognize the fact that in *A. fatua* after-ripening involves, in addition to physical changes of the coat, accompanying chemical alterations of the embryo itself.

IV. Summary

1. The germination of *A. fatua* has been found less delayed with the shell coats removed from the seed. However, with the shell coats removed, there exist after harvest germinative delays

which disappear with subsequent weeks. Hence the after-ripening of the seed occurs independent of the shell coats.

2. The after-ripening occurs along with the drying of the seed, but independent of the water content, as air-dried seed soon after harvest yields lower germinative percentages than seeds of similar moisture content the succeeding spring.

3. The germination seems unaffected by light.

4. Exclusion of water by the true seed coat does not seem to explain after-ripening.

5. The delay in germination is occasioned by restriction in the supply of oxygen, which thus acts as a limiting factor to germination. The seed coat is probably an obstruction to oxygen entry. This general situation seems pointed to by the combined results obtained by breaking and searing the seed coat; by removal of the embryo; by germinative percentages obtained in varying concentrations of oxygen, both below and above the normal of the air; by direct measurement of the rate of oxygen intake with intact and seared seeds, and with seeds in varying concentrations of oxygen.

6. The exact nature of the changes in the seed which constitute after-ripening cannot be stated positively. However, the data obtained seem to point to an increased permeability of the seed coat to oxygen, together with a rise in the embryo acid content, which is accompanined by increased water-absorbing power of the embryo.

I wish to acknowledge the cooperation of Dr. WILLIAM CROCKER who suggested the above problem, and has throughout been ready with helpful suggestions. I am also indebted to Miss ECKERSON for bibliographical material, and to my father, Mr. J. R. ATWOOD, for assistance in the tedious labor of preparing the seed for tests.

LITERATURE CITED

1. ABDERHALDEN, E., und DAMMHAHN, Über den Gehalt ungekeimter und gekeimter Samen verschiedener Pflanzenarten an peptolytischen Fermenten. Zeitschr. Physiol. Chem. **57**:332–338. 1908.

2. APPLEMAN, CHARLES O., Physiological behavior of enzymes and carbohydrate transformations in after-ripening of the potato tuber. BOT. GAZ. **52**:306–315. 1911.

3. ATTERBERG, ALBERT, Die Nachreife des Getreides. Landw. Versuchs-Stat. **67**:129–143. 1907.
4. BEAL, W. J., Vitality of seed. BOT. GAZ. **40**:140–143. 1905.
5. BLEISCH, C., Der Einfluss heisser Weichtemperaturen auf die Keimung der Gerste. Zeitschr. Gesells. Brau. **33**:538–539. 1910.
6. BOEHM, JOSEPH, Über die Respiration der Kartoffel. Bot. Zeit. **45**:671–675, 682–691. 1887.
7. BRIGHENTI, ALBERTO, Sull' autolisi delle sostanze vegetali. III. Contributo allo studio degli enzimi proteolitici nei semi non germinanti. Abst. in Zent. Biochem. und Biophysic. **14**:141. 1912.
8. ———, Nuovo contributo allo studio degli enzimi proteolitici nei semi non germinanti. Abst. in Zent. Biochem. und Biophysic. **14**:61. 1912.
9. BROWN, ADRIAN, J., On the existence of a semipermeable membrane enclosing the seeds of some of the Gramineae. Ann. Botany **21**:79–87. 1907.
10. ———, The selective permeability of the covering of the seeds of *Hordeum vulgare*. Proc. Roy. Soc. London B **81**:82–93. 1909.
11. ———, and WORLEY, F. P. The influence of temperature on the absorption of water by seeds of *Hordeum vulgare* in relation to the temperature coefficient of chemical change. Proc. Roy. Soc. London B **85**:546–553. 1912.
12. BROWN, HORACE T., and MORRIS, HARRIS, Untersuchungen über die Keimung einiger Gräser. Zeitschr. Gesells. Brau. **13**:375–380, 393–399, 417–429, 437–451, 477–481, 489–494. 1890.
13. BROWN, HORACE T., Die physikalische Beschaffenheit der Gerste vom anatomisch-physiologischen Standpunkt. Zeitschr. Gesells. Brau. **30**: 255–259. 1907.
14. CANNON, WILLIAM AUSTIN, A morphological study of the flower and embryo of the wild oat, *Avena fatua* L. Proc. Cal. Acad. III. **1**:329–355. *pls. 49–53*. 1900.
15. COUPIN, HENRI, Recherches sur l'absorption et le rejet de l'eau par les graines. Ann. Sci. Nat. Bot. VIII. **2**:129–222. 1896.
16. CRIDDLE, NORMAN, Wild oats and false wild oats; their nature and distinctive characters. Canada Dept. Agric. S. Bull. 7. pp. 11. *pls. 4*. 1912.
17. CROCKER, WILLIAM, The rôle of seed coats in delayed germination. BOT. GAZ. **42**:265–291. 1906.
18. ———, Germination of the seeds of water plants. BOT. GAZ. **44**:375–380. 1907.
19. DETMER, W., Über die Entstehung stärke umbildender Fermente in den Zellen hoherer Pflanzen. Bot. Zeit. **41**:601–606. 1883.
20. DEWEY, LYSTER H., Migration of weeds. Yearbook U.S. Dept. Agric. 277. 1896.
21. DUVEL, J. W. T., Preservation of seeds buried in the soil. Bot. Gaz. **37**:146–147. 1904.

22. ECKERSON, SOPHIA, A physiological and chemical study of after-ripening. Bot. Gaz. **55**:286–299. 1913.
23. FAWCET, H. S., The vitality of various weed seeds with different methods of treatment and investigations of their rest period. Proc. Iowa Acad. Sci. **15**:25–45. 1908.
24. FISHER, ALFRED, Wasserstoff und Hydroxylionen als Keimungsreize. Ber. Deutsch. Bot. Gesells. **25**:108–122. 1907.
25. GASSNER, GUSTAV, Über Keimungsbedingungen einiger südamerikanischer Gramineensamen. *Ibid.* **28**:350–364. 1910.
26. ———, Über Keimungsbedingungen einiger südamerikanischer Gramineensamen. *Ibid.* **28**:504–512. 1910.
27. ———, Vorläufige Mitteilung neuerer Ergebnisse meiner Keimungsuntersuchungen mit *Chloris ciliata*. *Ibid.* **29**:708–722. 1912.
28. ———, Untersuchungen über die Wirkung des Lichtes und des Temperaturwechsels auf die Keimung von *Chloris ciliata*. Jahrb. Hamburg. Wissenschaft. Anstalten **29**:1–120. 1911.
29. GREEN, J. REYNOLDS, On the germination of the castor oil plant. Proc. Roy. Soc. London B. **48**:370–392. 1890.
30. GRIS, A., Recherches sur la germination. Ann. Sci. Nat. Bot. V. **2**:5–123. 1864.
31. GRÜSS, J., Beiträge zur Physiologie der Keimung. Landw. Jahrb. **25**: 385–452. 1896.
32. GUERIN, P., Recherches sur le development du tégument séminal et du pericarpe des graminées. Ann. Sci. Nat. Bot. VIII. **9**:1–59. 1899.
33. GÜMBEL, HERMANN, Untersuchungen über die Keimungsverhältnisse verschiedener Unkrauter. Landw. Jahrb. **43**:215–321. 1912.
34. HAWKINS, LON A., The porous clay cup for the automatic watering of plants. Plant World **13**:220–227. 1910.
35. HEINRICHER, E., Die Samenkeimung und das Licht. Ber. Deutsch. Bot. Gesells. **26a**:298–301. 1908.
36. ———, Samenreife und Samenruhe der Mistel (*Viscum album* L.) und die Umstände welche die Keimung beinflussen. Anz. Ksl. Akad. Wiss. Wien, Math.-Naturw. Kl. **17**:258–259. 1912.
37. HOTTER, E., Über die Vorgänge bei der Nachreife von Weizen. Landw. Versuchs-Stat. **40**:356–364. 1892.
38. JANSON, C., Untersuchungen über die Einlagerung der Reservestoffe in die Hafer- und Gerstenkörner beim Reifungsprozess. Abst. in Bot. Centralbl. **110**:454. 1909.
39. JOHANNSEN, W., Studier over Planternes periodiske Livsyttringer. I. Om antagonistiske Virksomheder i Stofshiftet særlig under modning og Hoile. Abst. Bot. Jahrb. **25**:143. 1897.
40. JUNITZKEY, MELLE N., Respiration anaerobie des graines en germination. Rev. Gén. Botanique **19**:208–220. 1907.
41. KIESSLING, L., Untersuchungen über die Keimung der Getreide. Landw. Jahrb. (Bayern) **1**:449–514. 1911.

42. KINZEL, W., Über die Keimung halbreifer und reifer Samen der Gattung *Cuscuta*. Landw. Versuchs-Stat. **54**:125–133. 1900.
43. ———, Über den Einfluss des Lichtes auf die Keimung. "Lichtharte" Samen. Ber. Deutsch. Bot. Gesells. **25**:269–276. 1907.
44. ———, Die Wirkung des Lichtes auf die Keimung. *Ibid.* **26**[a]:105–115. 1908.
45. ———, Lichtkeimung. Einige bestätigende und ergänzende Bemerkungen zu den vorläufigen Mitteilungen von 1907 und 1908. *Ibid.* **26**[a]:631–645. 1908.
46. ———, Lichtkeimung. Erläuterungen und Ergänzungen. *Ibid.* **27**:536–545. 1909.
47. LEHMANN, ERNST, Über die Beeinflussung der Keimung lichtempfindlicher Samen durch die Temperatur. Zeitschr. Bot. **4**:465–529. 1912.
48. ———, Einige neuere Keimungsarbeiten. Sammelreferat. *Ibid.* **5**:365–377. 1913.
49. ———, und Ottenwälder, A., Über katalytische Wirkung des Lichtes bei der Keimung lichtempfindlicher Samen. *Ibid.* **5**:337–364. 1913.
50. LEPESCHKIN, W. W., Über die osmotischen Eigenschaften und den Turgordruck der Blattgelenkzellen der Leguminosen. Ber. Deutsch. Bot. Gesells. **26**[a]:231–237. 1908.
51. MUNERATI, O., and ZAPPAROLI, T. V., The influence of alternations of humidity and dryness on the germination of seeds in the case of some weeds. Malpighia **24**:313–328. 1912.
52. NILSSON-EHLE, H., Über Fälle spontanen Wegfallens eines Hemmungsfaktor bei Hafer. Zeitschr. Ind. Abst.- und Vererbungsl. **5**:1–37. 1911.
53. PAMMEL, L. H., The delayed germination of seeds. Rep. Brit. Assoc. Adv. Sci. (Winnipeg) 673–674. 1909.
54. ———, and KING, CHARLOTTE M., Delayed germination. Proc. Iowa Acad. Sci. **17**:20–33. 1910.
55. PUGLIESE, ANGELO, Sull 'autolisi delle sostanze vegetali. Nota IV. La formazione di amino-acidi e di ammoniaca nell 'autodigestione dei semi non germinanti. Abst. in Zent. Biochem. u. Biophysic. **14**:62. 1912.
56. QVAM, O., Zur Atmung des Getreides. Eine Relation zwischen Keimfähigkeit und Atmungsintensität. Jahresb. Verein Angew. Bot. **4**:70–87. 1906.
57. REICHARD, ALBERT, Der Gerbstoff in der Samenhaut des Gerstenkornes. Zeitschr. Chem. und Indus. Kolloide **10**:214–219. 1912.
58. RICHARDS, H. M., The respiration of wounded plants. Ann. Botany **10**:531–582. 1896.
59. SCHRÖDER, H., Über die selectiv permeable Hülle des Weizenkornes. Flora **102**:186–208. 1911.
60. SHULL, CHARLES ALBERT, The oxygen minimum and the germination of *Xanthium* seeds. BOT. GAZ. **52**:453–477. 1911.
61. ———, Semipermeability of seed coats. BOT. GAZ. **56**:169–199. 1913.

62. STICH, CONRAD, Die Atmung der Pflanzen bei verminderter Sauerstoffspannung und bei Verletzungen. Flora **74**:1–57. 1891.
63. STOWARD, F., On endospermic respiration in certain seeds. Ann. Botany **22**:415–448. 1908.
64. TRABUT, M., Contribution à l'étude de l'origine des avoines cultivées. Compt. Rend. **149**:227–229. 1909.
65. VAN TIEGHEM, PH., Recherches physiologiques sur la germination. Ann. Sci. Nat. Bot. V. **17**:205–224. 1873.
66. VOIGT, A., Flughafer. Jahresb. Verein Angew. Bot. **6**:290–294. 1908.
67. ZADE, ADOLPH, Der Flughafer. Inaug. Diss. Jena. pp. 1–48. 1909.
68. ZALESKI, W., Zur Kenntnis der Stoffwechselprozesse in reifenden Samen. Beih. Bot. Centralbl. **27**:63–82. 1911.

UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS XXXVIII[1]

JOHN DONNELL SMITH

Erysimum Ghiesbreghtii Donn. Sm.—Folia linearia apice calloso acuta deorsum angustata parce calloso-denticulata. Sepala pedicellis bis longiora, lateralia basi saccata. Petala obovata in unguem filoformem attenuata, lamina purpurea. Ovarium acute tetragonum, stylo brevi, stigmate bilobo.

Caules ex eodem rhizomate pluries simplices stricti 4–7 dm. longi rubescentes foliorum costa decurrente striati cum foliis racemo sepalis ovario pube bipartita plus minus strigillosi. Folia inferiora approximata 5–7.5 cm. longa 4–7 mm. lata, superiora sparsa decrescentia, suprema 2 cm. longa 3 mm. lata. Racemi 2.5 dm. longi sulcati, pedicellis 5–8 mm. longis. Sepala linearilanceolata 10–12 mm. longa 3 mm. lata costata, lateralia in saccam 1.5 mm. ongam producta. Petala 16 mm. longa, lamina 6 mm. lata saturate purpurea nervosa. Stamina 12 mm. longa. Pistillum petalis aequilonga, stylo 2 mm. longo, stigmate 1.5 mm. lato. Siliqua 3.7 cm. longa, valvis reploque carinatis, seminibus uniseriatis 12–15 immarginatis.

Inter saxa ad declivitates montis, Chiapas, Mexico, Aug. 1864–1870, *August Ghiesbreght*, n. 817.—Inter San Márcos et Ostuncalco, Depart. Quezaltenango, Guatemala, alt. 3000 m., Jun. 1882, *F. C. Lehmann*, n. 1510.

Xylosma chloranthum Donn. Sm.—Spinosum glabrum. Folia lanceolata tenuiter caudato-attenuata basi acuminata crenato-glandulariserrata nitida. Flores feminini umbellato-fasciculati pedunculis medio articulatis paulo longiores. Sepala 4 herbacea pistillo triente breviora. Ovarium tetragynum.

Frutex ad truncum ramosque vetustos spinis digitalibus compositis fuscis uti rami crebre lenticellato-punctatis armatus, ramulorum superiorum virgatorum spinis raris simplicibus tenuibus 6–8 mm. longis. Folia pergamentacea concoloria supra vernicoso-lucida 12–15 cm. longa 3–4 cm. lata ad caudam integra, nervis lateralibus utrinque 6–7, petiolo 5–7 mm. longo canaliculato. Pedunculi indefiniti 2–2.5 mm. longi, bracteis basalibus coacervatis squamiformibus ovatis 0.5–1 mm. longis margine puberulis. Sepala ex cl. repertore viridia ovata 2 mm. longa apice ipso puberula ceterum uti pistillum

[1] Continued from BOT. GAZ. 56:62. 1913.

glabra. Discus leviter crenatus. Ovarium ellipsoideum 2 mm. longum stylo bis longius, placentis 4 biovulatis, stigmatis lobis hippocrepiformibus. Flores masculini et baccae deficientes.

Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Apr. 1913, *H. von Tuerckheim*, n. 4111.

Sloanea (§ EUSLOANEA K. Schum.) **Tuerckheimii** Donn. Sm.—Folia ovalia basi acuminata subtus puberula. Racemi singuli simplices, rhachi gracili, pedicellis filiformibus, superioribus 2–3-nis. Stamina sepalis dimidio longiora, antheris quam filamenta bis brevioribus inappendiculatis rima apicali dehiscentibus. Discus intra torum staminalem nullus. Pistillum calyce bis fere longius.

Arbor, ramulis petiolisque teretibus, novellis fulvo-velutinis, denique pubescentibus. Stipulae caducae ignotae. Folia nascentia fulvo-velutina, adulta supra glabra 24–31 cm. longa 13.5–17.5 cm. lata cuspide deltoidea 5–8 mm. longa apiculata in angulum subrectum deorsum desinentia ad apicem versus obscure sinuato-dentata, nervis lateralibus utrinque 11–13 ante marginem anastomosantibus, venis transversis inter se summum 7 mm. distantibus, petiolis 4.5–6 cm. longis apice incrassatis. Racemi ad nodos plerumque defoliatos approximatos siti 8–13 cm. longi pubescentes, pedicellis 1.5–3.5 cm. longis, bracteis bracteolisque lanceolatis 3–5 mm. longis, floribus 1 cm.-diametralibus. Sepala 5–8 sublibera valvata oblongo- vel lanceolato-ovata circiter 4 mm. longa extus pubescentia intus fere glabra, maximo sepius 3-fido. Torus staminalis orbicularis 3 mm.-diametralis foveolatus. Stamina 6 mm. longa, antheris oblongo-ellipticis 2 mm. longis breviter apiculatis, filamentis patenter pubescentibus. Ovarium tetragono-ovoideum 2.5 mm. altum pilosum, stylo ad 1 mm. quadrifido. Capsula juvenilis ellipsoidea 1 cm. longa 0.5 cm. lata spinis 9 mm. longis puberulis setosa, matura ignota.—*S. multiflorae* Karst. valde affinis.

In silvis ad Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Mart. et Maj., 1913, *H. von Tuerckheim*, n. 4157.

Ilex (§ EUILEX Loesn.) **costaricensis** Donn. Sm.—Glabra. Folia elliptica breviter acuminata in petiolum angustata et decurrentia coriacea lucida impunctata subtus subtiliter glandulosa integra margine revoluta. Pedunculi solitarii 1–2–3-flori, floribus iso-pentameris. Ovarium ovoideum, stigmatibus sessilibus in hemisphaerium coalitis, loculis uniovulatis.

Ramuli annotini densissime foliati et pedunculi et pedicelli sulcato-angulati. Folia 4.5–6.5 cm. longa 2.5–3.5 cm. lata, nervis lateralibus fortioribus utrinque 7–8, petiolis 1.5–2 cm. longis canaliculatis, stipulis squamae-

formibus deltoideis minutis. Pedunculi axillares vel superiores extra-axillares 8–14 mm. longi, pedicellis singulis vel 2–3-nis 6–8 mm. longis, bracteis stipulae-formibus, floribus tantum femininis notis. Calycis partiti lobi semi-orbiculares 1 mm. longi. Petala subquadrata 3.5 mm. longa atque lata usque ad 1 mm. fere connata. Antherae cassae orbiculares, 1 mm.-diametrales filamento paulo longiores. Ovarium 2 mm. longum stigmatum hemisphaerio bis longius. Drupa deficiens.—*I. mexicanae* (Turcz.) Benth. et Hook. quoad inflorescentiam proxima videtur.

Cuesta dela Cara, haud procul ab El Páramo, Comarca de Puntarenas, Costa Rica, Jan. 1897, *H. Pittier*, n. 10843.

Connarus brachybotryosus Donn. Sm.—Foliola 3 elliptica vel ovato-elliptica cuspidato-acuminata apice ipso obtusa basi rotundata bis longiora quam latiora nitida. Racemi fasciculati petiolo breviores. Sepala petalis paulo breviora staminibus longioribus 3-plo longiora pistillo aequilonga.

Arbor. Folia glaberrima petiolo 6–8 cm. addito 2.5–3 dm. longa, foliolis 1.5–2 dm. longis coriaceis, nervis lateralibus fortioribus utrinque 5 subtus elevatis. Racemi paucifasciculati 4–5 cm. longi cum sepalis ferrugineo-pubescentes, pedicellis 2–3 mm. longis, floribus ex cl. repertore luteo-viridibus. Sepala discreta oblongo-ovata 3 mm. longa. Petala obovato-oblonga 4 mm. longa 1.5 mm. lata glabra. Stamina longiora 1 mm. longa, breviorum antheris subsessilibus. Ovarium lanceolato-ellipsoideum 1.5 mm. longum cum stylo aequilongo appresse pilosum, stigmate 5-capitellato. Capsula ignota.

In silvis ad Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Febr. 1913, *H. von Tuerckheim*, n. 4027.

DALBERGIA VARIABILIS Vog., var. **cubilquitzensis** Donn. Sm.—Petiolus communis usque ad 2 dm. longus, foliolis oblongis 8.5 cm. longis 3-plo et ultra longioribus quam latioribus. Cymae fusco-pubescentes 6.5 cm. latae. Stamen vexillare deficiens. Ovarium vacuum.

Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Febr. 1913, *H. von Tuerckheim*, n. 4091.

Drepanocarpus (§ RETICULATI Benth.) **costaricensis** Donn. Sm.—Stipulae triangulares spinescentes. Foliola 9–15 oblonga vel elliptica apice late acuta mucronulata basi rotundata supra araneosa subtus fulvo-tomentosa. Flores sessiles, bracteolis calycis duas partes cingentibus. Calycis dentes superiores late rotundati, inferiores anguste triangulares. Vexillum crassum extus sericeum. Stamina iso-diadelpha.

Ramuli juniores cum stipulis petiolis foliolorum pagina inferiore paniculis fulvo-tomentosis, bracteolis calyce vexillo fulvo-sericies. Stipulae 5 mm. longae deciduae. Petiolus communis 10.5–13 cm. longus, foliolis reticulato-nervosis plerumque oblongis 4.5–7.5 cm. longis 1.5–2.5 cm. latis, inferioribus cujusque folii decrescentibus magis ellipticis 3 cm. longis 2 cm. latis, terminali maximo obovato-oblongo. Paniculae in exemplis mancis solum suppetentibus axillares singulae folia superantes, bracteolis subsemiorbicularibus 4 mm. longis persistentibus, floribus 11 mm. longis. Calyx 6 mm. longus, dentibus 2 mm. longis, superioribus 3 mm. latis. Vexillum subcoriaceum suborbiculare 9 mm. longum atque latum alis aequilongum. Stamina carinam cucullatam 7 mm. longam aequantia, vagina jam in alabastro utrinque usque ad basin fissa. Ovarium basi disco cupulari cinctum leviter incurvum villosum uniovulatum, stylo brevissimo. Legumen deficiens.—Ad. *D. salvadorensem* Donn. Sm. floris indole accedens foliis praesertim recedit.

Santiago prope San Ramón, Prov. Alajuela, Costa Rica, alt. 1000–1100 m., Jun. 1901, *Amando Brenes*, n. 14507.—Typus in herbario Musei Nationalis sub numero proprio 861757 servatur.

Lonchocarpus santarosanus Donn. Sm.—Foliola 13–15 lanceolato- vel oblongo-ovata apice tenuiter acuminata basi acuta vel obtusa impunctata. Pedicelli approximati solitarii biflori pedicellis propriis additis florem subaequantes. Vexillum subsemiorbiculare pubescens. Alae et carina rectae exauriculatae. Ovarium biovulatum demum monospermum.

Arbor 6–8-metralis, ramulis novellis petiolulis foliolorum subtus nervis pedicellis calyce ferrugineo-pubescentibus. Petiolus communis 13–18 cm. longus glabrescens. Foliola plerumque 6-juga 4.5–6.5 cm. longa 2–2.5 cm. lata chartacea supra glabra subtus pubescentia, nervis lateralibus utrinque 5–6, petiolulis 4–5 mm. longis. Racemi 6–9 cm. longi supra medium floriferi, pedicellis communibus circiter 4 mm. longis raro 3-floris, pedicellis propriis 2–3 mm. longis infra apicem bracteolatis, bracteis bracteolisque orbicularibus vix 0.5 mm. longis caducis. Calyx late campanulatus 2 mm. longus truncatus. Petala coccinea, vexillo 6 mm. longo latiore quam longiore basi latissime acuto prope unguem transverse bicalloso, alis carinaque late oblongis basi truncatis. Tubus stamineus 4 mm. longus. Ovarium pubescens. Legumen mihi non visum.

Mataquescuintla, Depart. Santa Rosa, Guatemala, alt. 1560 m., Mart. 1894, *Heyde et Lux*, n. 6328 ex Pl. Guat. etc. quas ed. Donn. Sm.

CAESALPINIA BONDUCELLA Fleming, var. **urophylla** Donn. Sm.—Petiolus communis 2 dm. longus glaber seta terminatus, foliolis 7-jugis oblongo-ellipticis 6–8.5 cm. longis 3–3.5 cm. latis caudato-

acuminatis seta mucronatis basi rotundatis chartaceis nitidis. Racemus axillaris 22 cm. longus, bracteis patentibus 5 mm. longis, floribus 1.5 cm. longis submasculinis. Calycis tubus obliquus sulcatus 7 mm. longus, segmenta 8–10 mm. longa. Petala nigro-nervosa. Filamenta infra medium villosa.—Exemplum unicum mihi visum quamquam imperfectum varietatem tamen insignem vel forsitan speciem novam constituere videtur.

Ad collem San Isidro prope San Ramón, Prov. Alajuela, Costa Rica, alt. 1300 m., Jul. 1901, *Amando Brenes*, n. 14501.—Typum in herbario Musei Nationalis sub numero proprio 861756 vidi.

Leucaena Shannoni Donn. Sm.—Pinnae 4–5-jugae, foliolis 9–15-jugis oblongis apice rotundato mucronulatis basi rotundatis inaequilateralibus binerviis, superioribus obovato-oblongis basi gibboso-obliquis, petiolo sicut pinnarum rhachis prope apicem glandula oblonga munito. Racemus terminalis elongatus, pedunculis 2–5-nis, floribus glabris.

Petiolus communis 6–8.5 cm. longus teres pubescens. Pinnarum rhachis 6–10 cm. longa lineis duabus pubescentibus a foliolis decurrentibus angulata. Foliola 15–22 mm. longa 5–8 mm. lata pubescentia vel glabrescentia utrinque conspicue nervosa. Racemus 2–4 dm. longus crassus aphyllus glabrescens glanduligerus, pedunculis 12–22 mm. longis pubescentibus apice vel infra apicem bracteis quaternis minutis instructis, capitulis absque staminibus 1 cm.-diametralibus. Calyx turbinatus 2 mm. longus. Petala spatulato-lanceolata 3 mm. longa. Stamina 6 mm. longa, antheris oblongis 1 mm. longis. Stylus 2 cm. longus. Legumen haud satis maturum tantum visum breviter (8 mm.) stipitatum 10 cm. longum 12 mm. latum utrinque acuminatum suturis pubescens, seminibus oblique transversis.

Cojutepeque, Depart. Cuscatlán, Salvador, alt. 900 m., Dec. 1892, *W. C. Shannon*, n. 5032 ex Pl. Guat. etc. quas ed. Donn. Sm.—Eadem planta a *C. B. Doyle* ad Rosario, Chiapas, Mexico, Dec. 1906 lecta, sub numero 87[a] distributa, in herbario Musei Nationalis numero proprio 574705 signata exstat.

Pithecolobium (§ SAMANEA Benth.; *Parviflora* Benth.) **adinocephalum** Donn. Sm.—Pinnae 1–2-jugae, foliolis 3–5-jugis lanceolato- vel ovato-oblongis apice ipso obtusis basi acutis centrali-costatis coriaceis supra nitidis subtus puberulis pallidioribus, glandula infra medium petioli oblonga inter foliola parium 1–2 superiorum scutelliformi. Panicula densissime capitulifera, pedunculis radiatim fasciculatis, floribus pedicellatis.

Arbor inermis, coma rotundata, ramulis teretibus glabris. Petiolus communis 2–7 cm. longus cum pinnis 4–7 cm. longis tetragonus glaber, foliolis 2.5–4.5 cm. longis 1–2 cm. latis, nervis lateralibus late patentibus, venis supra conspicuis minute reticulatis. Panicula terminalis 10–14 cm. longa, ramis striatis, infimis 6–9 cm. longis erecto-patentibus, pedunculis 3–6-fasciculatis gracilibus 1.5–2 cm. longis puberulis, capitulis absque staminibus 7 mm.-diametralibus, pedicellis 1 mm. longis puberulis. Calyx campanulatus 1 mm. longus puberulus. Corolla infundibuliformis 3 mm. longa. Stamina in tubum inclusum connata 8 mm. longa. Legumen junius solum visum rectum planum glabrum 1.5 dm. longum 2 cm. latum, seminibus circiter 13.—*Gabiloncillo* incolarum.

Ad fundum *La Verbena* prope Alajuelita, Prov. San José, Costa Rica, alt. 1000 m., *Ad. Tonduz;* Aug. 1894, n. 8932; Dec. 1894, n. 9077.—In silvis collinis, Peninsula Nicoya, Costa Rica, Jan. 1900, *Ad. Tonduz*, n. 13531.

Guamatela Donn. Sm., nov. gen. ROSACEARUM e tribu SPIRAEEIS Focke.—Flores hermaphroditi. Calycis persistentis tubus brevis, segmenta 5 imbricata. Petala 5 ori calycis inserta. Stamina 10 uniseriata segmentis calycinis et petalis opposita, filamentis liberis, antheris cordato-ovatis apiculatis. Discus tubum calycis vestiens concavus margine integro petala et stamina ferens. Carpidia 3 sessilia ope stigmatorum primum connata demum libera, stylis terminalibus, stigmatibus capitellatis, ovulis pluribus suturae ventrali biseriatim affixis ascendentibus. Carpidium seminiferum unicum membranaceum sutura ventrali dehiscens, seminibus pluribus obovoideis exalbuminosis, testa ossea nitida.—Frutex reclinans. Folia opposita simplicia cordato-ovata serrulata palmatinervia. Stipulae liberae setaceae. Racemi terminales, bracteis filiformibus, floribus sanguineis.—Genus foliis oppositis in *Spiraeeis* anormale.—Nomen ope metatheseos syllabarum patriam significat.

Guamatela Tuerckheimii Donn. Sm.—Folia supra glabra viridia bullata subtus niveo-tomentosa 5–7-nervia. Racemi singuli vel bini, pedicellis alternis, inferioribus saepe 3-floris. Calycis segmenta oblongo-ovata acuta. Petala oblongo-elliptica et stamina calyce breviora. Carpidia lanceolato-ovoidea, duobus tertio jam sub anthesi paulo minoribus denique vacuis marcidis. Folliculus subovalis inflatus, stylo incurvo.

Caulis ramosus, ramulis petiolis foliorum utrinque nervis fusco-pubescentibus. Stipulae 2–4 mm. longae. Folia longe tenuiterque acuminata 4.5–9 cm. longa 2.5–5.5 cm. lata, petiolis 0.5–2.5 cm. longis. Racemi

adjecto pedunculo 2.5–4 cm. longo 9–10 cm. longi niveo-tomentosi circiter 10–16-flori, pedicellis 4–5 mm. longis, bracteis binis 6–8 mm. longis. Calycis sanguinolenti tubus 2 mm. longus, segmenta 7 mm. longa striata utrinque incana. Petala 5 mm. longa vix unguiculata nervosa utrinque pubescentia. Filamenta 4 mm. longa e basi superne decrescentia, antheris aegre 1 mm. longis. Carpidia incana sub anthesi 4 mm. longa, stylis rectis 2 mm. longis. Folliculus nondum satis maturus solum suppetens 7 mm. longus 5 mm. latus, seminibus circiter 11–12 imbricatis 1.2 mm. longis atque crassis.

In silvis montanis prope Purulhá, Depart. Baja Verapaz, Guatemala, alt. 1750 m., Oct. 1912, *H. von Tuerckheim*, n. 3903.

Rubus (§ EUBATUS Focke.) **leptosepalus** Donn. Sm.—Foliola quinata orbiculari-ovalia acute caudato-acuminata basi rotundata, ternata ovato- vel obovato-elliptica acuminata basi obtusa vel acuta. Paniculae angustae nutantes laxiflorae superne simpliciter foliatae, bracteis setaceis perlongis. Sepala lineari-lanceolata setaceo-appendiculata petalis suborbicularibus aequilonga.

Rami digitulum crassi subtetragoni sulcati glandulifero-setosi cum ramulis petiolis petiolulis paniculis glandulifero-pilosis recurvo-aculeati rubiginoso-pubescentes. Stipulae petiolares setaceae 10–12 mm. longae. Foliorum inferiorum foliola quinata 10–14 cm. longa 5.5–8.5 cm. lata argute duplo-serrata membranacea supra glabrescentia subtus pubescentia nervo medio aculeata, petiolis 7–8 cm. longis, petiolulo intimo 4.5 cm. longo, extimis 12 mm. longis. Foliorum superiorum foliola ternata 6–10.5 cm. longa 3–5 cm. lata, petiolo 1–2 cm. longo, petiolulis 6–15 mm. longis. Ramuli floriferi erecto-patentes. Paniculae parce minuteque aculeatae rami inferiores breves, superiores subsecundi foliis lanceolatis 4–6 cm. longis interdum suffulti, bracteis 1.5–2.5 cm. longis uti bracteolae 6 mm. longae extus cano-pubescentibus. Sepala appendicula 4–5 mm. longa computata 1.5–1.7 cm. longa utrinque cano-tomentulosa eglandulosa inermia. Petala ex cl. repertore rosea. Receptaculum ovideum 4 mm. longum. Germina numerosa glabra. Fructus desideratur.—*R. adenotricho* Schlecht. habitu affinis sepalis praesertim differt.

Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350 m., Jul. 1912, *H. von Tuerckheim*, n. 2452.

Gilibertia leptopoda Donn. Sm.—Folia integra lanceolata vel lanceolato-elliptica tenuiter acuminata basi acuta. Umbellae terminales racemosae, pedunculis paucis longissimis filiformibus inarticulatis nudis, pedicellis paucis elongatis, floribus 5–6-meris. Calyx turbinatus margine subinteger. Petala triangulari-ovata staminibus paulo longiora.

Arbor. Folia 10.5–13 cm. longa 3.5–4 cm. lata pergamentacea rubropunctulata, nervis lateralibus fortioribus utrinque 7–8 et venis inconspicuis, petiolis summum 4 cm. longis. Racemi rhachis 2–3 cm. longa, pedunculis 5–7 cm. longis ad apicem rhacheos 4–6-fasciculatis infra apicem 1–4 sparsis sub insertione pedicellorum vix dilatatis, pedicellis 3–8-nis 14–16 mm. longis, bracteis bracteolisque vix ullis. Calyx 2 mm. longus in pedicellum attenuatus. Petala 1.5 mm. longa apiculata striata. Antherae orbiculares 1 mm. longae filamenta aequantes. Discus leviter convexus. Styli in conum brevissimum fere connati. Fructus non suppetit.—Secundum clavem specierum Centrali-Americanarum in BOT. GAZ. **55**:436. 1913 adumbratam haec juxta *G. Rothschuii* Harms locanda discrepat inter alia umbellis paucifloris.

In silvis montanis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1550 m., Jan. 1913, *H. von Tuerckheim*, n. 4166.

Faramea (§ TETRAMERIUM DC.) **cobana** Donn. Sm.—Folia lanceolata apice ipso obtusa basi acuminata. Stipulae triangulares aristulatae costa decurrentes. Pedicelli in axibus superioribus fasciculati pedunculo vix ullo insidentes floribus subaequilongi. Calycis eglandulosi limbus denticulatus tubo 3-plo brevior. Corolla triente lobata. Antherae inclusae. Bacca globosa ecostata.

Fruticulus metralis totus glaberrimus, ramulis decursu stipularum bicarinato-angulatis. Folia 5.5–7.5 cm. longa 13–21 mm. lata pergamentacea opaca, costa utrinque prominente, nervis lateralibus patulis utrinsecus 9–11, petiolo 2–3 mm. longo, stipulis e basi crassa 1–2 mm. longa in aristam 3–5 mm. longam sensim productis. Pedunculus 1–2 mm. longus, pedicellis 2–3-nis filiformibus 12 mm. longis. Calyx 2 mm. longus, tubo turbinato, limbo urceolato, denticulis minutis. Corolla (nondum satis aperta solum visa) 12 mm. longa ex schedula coerulea, tubo gradatim dilatato infra medium staminigero, lobis oblongo-ovatis. Antherae subsessiles prope basin affixae 4 mm. longae. Discus limbum calycinum aequans. Stylus 7 mm. longus. Bacca 9 mm.-diametralis saturate atricolor ex cl. repertore, semine sphaerico 6 mm.-diametrali basi profunde excavato, albumine cyaneo.—Juxta *F. pedicellarem* Muell. Arg. locanda.

In silvis montanis oppido *Cobán* vicinis, Depart. Alta Verapaz, Guatemala, alt. 1550 m., Jul. 1912, *H. von Tuerckheim*, n. 2474.

Farameae clavis specierum Centrali-Americanarum.

Sect. I. HYPOCHASMA Muell. Arg.

A. Folia penninervia.

1. Calyx denticulatus.....*F. salicifolia* Presl.
2. Calyx inaequaliter lobatus.....*F. eurycarpa* Donn. Sm.

B. Folia trinervia.
1. Folia auriculata.....*F. trinervia* K. Schum. et Donn. Sm.
2. Folia basi acuta.....*F. suerrensis* Donn. Sm.

Sect. II. TETRAMERIUM DC.
A. Inflorescentia corymbosa.....*F. odoratissima* DC.
B. Inflorescentia fascicularis.....*F. cobana* Donn. Sm.

Jacquemontia (§ CYMOSAE Meissn.) **platycephala** Donn. Sm.—Folia cordato-ovata supra glabra subtus minute strigillosa. Pedunculi folia non aut parum superantes. Cyma transversim oblongo-capituliformis compacti-flora imbricato-bracteosa fusco-villosa, bracteis extimis orbicularibus, interioribus oblongo-obovatis. Sepala elliptica acuminata bracteis intimis triente corolla triplo breviora.

Volubilis, caulibus petiolis pedunculis appresse pilosis vel glabrescentibus. Folia 6.5–7.5 cm. longa 4–5 cm. lata mucrone apiculata, nervis lateralibus utrinque 8–9 subtus conspicuis usque ad marginem distinctis, petiolis 2.5–3 cm. longis. Pedunculi 9–13 cm. longi. Cyma (nondum profecto evoluta tantum visa) corollis neglectis 2.5–3 cm. alta 7–9.5 lata, ramis lateralibus brachiatis elongatis, intermedio vix ullo, floribus numerosis subspicatis secundis, bracteis uti sepala extus fusco-villosis intus glabris nigricantibus, extimis duabus 18–20 mm.-diametralibus, interioribus pluribus 17–20 mm. longis 8–10 mm. latis. Sepala cymbiformia 12–13 mm. longa 6–7 mm. lata. Corolla 38 mm. longa ad plicas fusco-villosa ex schedula alba. Stamina ad 10 mm. supra basin corollae inserta 12 mm. longa, antheris 4 mm. longis. Ovarium pilosum, stylo 18 mm. longo, stigmate capitato-bilobo. Capsula ignota.—*Ipomoeae hirtiflorae* Mart. et Gal. et *I. Perryanae* Duchass. et Walp., speciebus ambabus ob inflorescentiam ad *Jacquemontiam* melius ascribendis, nostra valde affinis videtur.

Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Apr. 1913, *H. von Tuerckheim*, n. 4133.

Cyphomandra aculeata Donn. Sm.—Omnibus in partibus glabra. Folia solitaria lanceolato-oblonga utrinque acuminata, costa subtus et petiolo aculeatis. Cyma pauciflora. Corolla calyce 3-plo longior rotata. Stamina recta basi connata, filamentis brevibus deorsum dilatatis, connectivo sub antherae apice evanido. Stylus filiformis, stigmate clavato.

Folia in ramulo unico suppetente 8–10.5 cm. longa 2.3–3 cm. lata chartacea, nervis lateralibus utrinsecus 7–8, petiolis 11–14 mm. longis, aculeis minutis recurvis. Cymae unicae vistae pedunculus 4 cm. longus, axes pri-

mariae 7–10 mm. longae, pedicelli 2.5–3 cm. longi, flores 4 circiter 22 mm. longi. Calyx 7 mm. longus, lobis 3 mm. longis semiorbicularibus. Corollae tubus 4 mm. longus, segmenta anguste oblonga 15–16 mm. longa basi 4 mm. lata superne sensim acuteque angustata crassa. Stamina 14 mm. longa in annulo 2 mm. longo connata, filamentis 3 mm. longis triangularibus, antheris anguste oblongis 9 mm. longis, connectivo crasso 2 mm. lato ecalloso. Stylus 6 mm. longus. Bacca ignota.

Prope Cobán, Depart. Alta Verapaz, Guatemala, Apr. 1882, *F. C. Lehmann*, n. 1334.

Brachistus meianthus Donn. Sm.—Omnibus in partibus praeter corollam et stamina glaberrimus. Folia attenuato-acuminata in petiolum oblique attenuata gemina, altero lanceolato-elliptico, altero 2–3-plo minore rhomboideo-ovato. Flores 4–5-meri. Calyx integer. Corollae segmenta tubo intus pubescente bis longiora extus puberula. Antherae cordiformes filamenta pubescentia subaequantes. Bacca coccinea.

Fruticosus, ramulis teretibus. Folia membranacea pellucida minute punctulata integerrima, altero 11–15 cm. longa 3.5–5.3 cm. lata petiole 1.7–2.1 cm. longo, nervis lateralibus utrinque 5–6 sicut venae transversae remotae subtus conspicuis, altero 3.5–6 cm. longo 2–3 cm. lato, petiolo 3–6 mm. longo. Pedunculi pluri-fasciculati nonunquam semel dicotomi, floriferi 12 mm. longi, fructiferi 15 mm. longi. Calyx hemisphaericus 1 mm. altus. Corolla 5–6 mm. longa ex schedula flavicans, tubo ad insertionen, staminum pubescente, segmentis oblongo-ovatis. Stamina 4 mm. longa, antheris acutis. Stylus corollam paulo superans. Bacca calyci immutato insidens globosa 6–7 mm.-diametralis.—*B. hebephyllo* Miers. proximus.

Pansamalá, Depart. Alta Verapaz, Guatemala, alt. 1250 m., Febr. 1887, *H. von Tuerckheim*, n. 1134 ex Pl. Guat. etc. quas ed Donn. Sm.—In silvis ad Panzal, Depart. Baja Verapaz, Guatemala, alt. 1350 m., Oct. 1912, *H. von Tuerckheim*, n. 3936.

Columnea (§ EUCOLUMNEA Hanst.) **cobana** Donn. Sm.—Valde anisophylla. Folia subsessilia lanceolato-oblonga vel -elliptica attenuato-acuminata basi inaequali acuta supra glabra subtus nervis marginibusque pilosa ceterum sparsim strigillosa. Pedunculi folio majore paulo breviores. Calycis segmenta attenuato-ovata dentata. Corolla calycem 4-plo superans, tubo limbum aequante, galea truncata integra.

Fruticulus epiphytalis. Caules subtetragoni radicantes, novelli sicut petioli et pedunculi pilis patentibus articulatis rubro-tinctis hirsuti. Folium in pare majus 6–7.5 cm. longum 1.5–2 cm. latum, alterum 18–30 mm. longum

8–13 mm. latum, nervis lateralibus utrinque 4–5, venis obsoletis, petiolis 1–2 mm. longis. Pedunculi singuli 4–6 cm. longi fuscescentes. Calycis obliqui viridis segmenta 1.5 cm. longa 7 mm. lata pilosa, dentibus utrinque 4 obtusis glandula apiculatis. Corolla coccinea extus pilosa intus rubro-granulifera 6–6.5 cm. longa basi gibbosa, lobo antico triangulari-oblongo obtuso 16 mm. longo 7 mm. lato, lateralibus obtuse deltoideis cum galea ad 13 mm. connatis margine superiore 8 mm. longis, galea propria 18 mm. longa 15 mm. lata. Stamina galeam usque ad 7 mm. superantia, antheris subquadratis 3 mm. longis. Disci glandula unica quadrata 1.5 mm. longa bifida. Ovarium ovoideum 4 mm. altum pilosum, stylo rubro cum staminibus supra medium puberulo, stigmate integro.—Ad *C. magnificam* Klotzsch et Hanst. floribus accedens.

In silvis montanis ad Cobán, Depart. Alta Verapaz, Guatemala, alt. 1550 m., Jul. 1912, *H. von Tuerckheim*, n. 2475.

Columnea (§ EUCOLUMNEA Hanst.) **lutea** Donn. Sm.—Folia leviter disparia subsessilia ovato- vel subrhomboideo-oblonga inaequilatera apice acuta basi obtusa vel retusa integra margine revoluta supra cano-strigillosa subtus nervis pilosa. Calycis segmenta obovato-elliptica nervosa utrinque viridia et cano-villosa. Corolla lutea. Disci glandula minima bidentata.

Fruticosa, caulibus ascendentibus approximatis pluribus teretibus, novellis et pedunculis patenter fusco-pilosis. Folia 2–3 cm. longa 10–12 mm. lata, nervis lateralibus utrinque 4–5, venis obsoletis, petiolis 1mm. longis. Pedunculi singuli 11 mm. longi. Calycis segmenta 1 cm. longa 4 mm. lata. Corolla ex cl. repertore lutea extus arachnoidea intus glabra circiter 6 cm. longa incurva basi leviter gibbosa, lobo antico lanceolato-lineari 24 mm. longo 4 mm. lato, lateralibus cum galea usque ad ejus duas partes connatis margine superiore 6 mm. longis, galea propria 12 mm. longa explanata 15 mm. lata fornicata emarginata genitalia superante. Stamina glabra, antheris 2 mm. longis 1.5 mm. latis. Disci glandula vix 0.5 mm. longa. Ovarium cano-pilosum, stylo complanato bifariam puberulo, stigmatis lamellis ovatis 2 mm. longis. Bacca globosa 7 mm.-diametralis calyce accrescente bis superata, glandula 1.5 mm. longa.—Ad *C. microcalycem* Hanst. floris structura accedens colore abhorret.

Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Febr. 1901, *H. von Tuerckheim*, n. 7930 ex Pl. Guat. etc. quas ed. Donn. Sm.

Aegiphila (§ CYMOSAE Schau.; *Subtruncatae* Briq.) **fasciculata** Donn. Sm.—Folia longiuscule petiolata opposita lanceolato-oblonga utrinque acuminata supra bulboso-pilosa subtus ochraceo-tomentosa. Cymae femininae sessiles, axibus obsoletis, floribus fasciculatis. Calyx truncatus 4-mucronulatus. Stamina ananthera.

Arbor, ramulis subtetragonis sicut petioli foliorum subtus nervi bracteae pedicelli calyces ochraceo-velutinis, internodiis superioribus 2–3 cm. longis. Folia 15–22 cm. longa 5.5–7.5 cm. lata tenuiter acuminata medio latissima, nervis subtus elevatis conspicuis, lateralibus utrinsecus 6–7, petiolis 2–3.5 cm. longis. Flores solum femini suppetentes in axillis subglomerati subsessiles 4-meri, bracteis linearibus 6–12 mm. longis convolutis deciduis, pedicellis 1–2 mm. longis. Calyx turbinato-campanulatus 6–7 mm. longus minute mucronulatus. Corolla infundibuliformis 9–10 mm. longa alba cum genitalibus glabra, lobis tubum intus furfuraceum aequantibus ovatis acutis. Stamina ad 2 mm. supra basin tubi inserta subulata 1 mm. longa. Stylus 12 mm. longus triente bifidus, ramis papillosis. Drupa ignota.—*A. tomentosae* Cham. quoad inflorescentiam proxima.

In silvis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350 m., Dec. 1912, *H. von Tuerckheim*, n. 4013.

Aegiphilae clavis specierum Centrali-Americanarum.

I. Cymae axillares.
  A. Cymae sessiles.....*A. fasciculata* Donn. Sm.
  B. Cymae pedunculatae.
    1. Cymae densiflorae.....*A. arborescens* Vahl.
    2. Cymae laxiflorae.
      a) Folia opposita.....*A. odontophylla* Donn. Sm.
      b) Folia verticillata.....*A. anomala* Pittier.

II. Thyrsi axillares et terminales.
  A. Calyx truncatus.
    1. Rami subteretes.....*A. martinicensis* L.
    2. Rami acute tetragoni.....*A. falcata* Donn. Sm.
  B. Calyx lobatus.
    1. Corolla infundibuliformis.....*A. brachiata* Schlecht.
    2. Corolla hypocrateriformis.....*A. elata* Sw.

Scutellaria (§ VULGARES Benth.; *Coccineae* Briq.) **isocheila** Donn. Sm.—Folia lanceolato-oblonga utrinque acuminata vel acuta sinuato-dentata discoloria praeter nervos subtus fusco-puberulos glabra. Racemi foliis breviores densiflori, bracteis lanceolatis, inferioribus pedicello 2–3-plo longioribus, superioribus eo brevioribus. Corolla usque ad fauces graciliter tubulosa aequaliter bilabiata.

Fruticulus erectus semimetralis parce ramosus, ramis subtetragonis cum petiolis racemis calyce fusco-puberulis. Folia 6–8 cm. longa 2–2.5 cm. lata subtus pallida, nervis lateralibus utrinque 4–5, petiolis 8–11 mm. longis. Racemi terminales floribus ademptis 2–3 cm. longi 12–16-flori, bracteis

foliaceis, infimis 8 mm. longis, superioribus minutis, pedicellis 2–3 mm. longis, floribus oppositis secundis. Calyx 4 mm. longus, scutello 2 mm. longo. Corollae roseae pubescentis tubus 2.5 cm. longus, labia 3 mm. longa, lobi erecti integri, laterales cum postico breviter coaliti eum aequantes. Stamina majora 12 mm. longa alteris bis longiora, antheris canescentibus eciliatis, loculis omnibus polliniferis. Nuculae deficientes.—*S. Lindenianae* Benth. ex char. proxima.

In silvis humidis ad Cerro de Carizia, Prov. Heredia, Costa Rica, alt. 1800 m., Sept. 1900, *H. Pittier*, n. 16128.

Baltimore, Md.

THE OVARY AND EMBRYO OF CYRTANTHUS SANGUINEUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 186

MARGARET ELIZABETH FARRELL

(WITH PLATE XXIV AND THREE TEXT FIGURES)

Cyrtanthus sanguineus Hook. (Amaryllidaceae) is one of the 37 species credited to the genus. It was first figured in the *Botanical Magazine* (1), and was copied by PAX (2) in his monograph of the family. The genus is restricted to South Africa. *C. sanguineus* and two other species were procured by Dr. C. J. CHAMBERLAIN from the Botanical Garden at Durban, a garden which, like most of those of the colonies, is supported by the nursery trade. The plants are not raised from seed in the garden, but are brought there after being dug up from places in which they grow naturally. The plants secured by Dr. CHAMBERLAIN have been growing in the greenhouses of the University of Chicago. The first blossoms appeared in the winter of 1912–1913. They were hand-pollinated, and from the ovaries and embryos thus derived the present study was made.

Cyrtanthus sanguineus has a tunicated bulb about two inches in diameter. The leaves are thick and leathery, of a bright green color, and about a foot long. The epigynous flower is 3–4 inches in length, and of a rich coral color, almost crimson. The perianth tube is either suberect or decidedly curved, and the upper half of its throat is about one inch in diameter. The stamens are uniseriate and slightly exserted; the filaments are incurved and the anthers are oblong. The ovary is 18 cm. long and 6 cm. in diameter. The ovules are campylotropous. In an ovary of about 12 ovules only 6 or 7 develop to maturity.

Ovary

The material was taken at different ages, killed in chromacetic fluid, and the sections stained in safranin and gentian. All the drawings were made with the help of an Abbé camera lucida.

The ovary is composed of three carpels. I found two different arrangements of their vascular bundles according to location. In the region of the lateral fusion of the carpels, there are three bundles grouped as one. All are collateral; the outer one is ectophloic, and the other two are so arranged that their xylem masses face each other (text fig. 1). The strands at the midrib of each carpel appear in three distinct groups; the outermost one consisting of a single collateral ectophloic bundle; the innermost one of two bundles with their xylem masses facing; and the intervening group composed of two double bundles, the degree of approximation of which differs at different levels in the carpel. One of the levels is shown in text fig. 2. This peculiarity of arrangement is probably due to the curving of the edge of the carpels to form the closed ovary. A closer study led to an explanation of the different groups of bundles, and showed that each organ of the flower is supplied from these vascular strands. Text fig. 3 is a diagram of the flower, the dotted line representing the outline of the ovary. It can be seen that the abortion of the stigmas occurred opposite the region of the fusion of carpels. On tracing their bundles downward into the ovary, they are found to be derived from the primary groups in the carpel. Lower still, these bundles fuse with those of the flower stem.

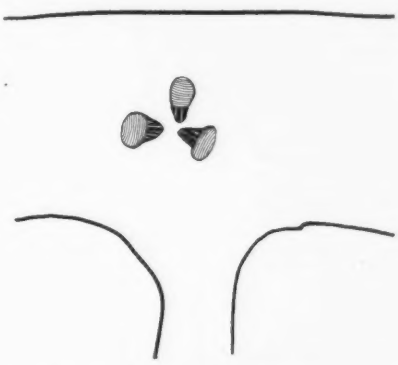


FIG. 1.—Showing the vascular arrangement at the fusion of the carpels.

Noticing the frequent occurrence of stomata on the inner surface of the carpels, I was interested to know the relative number per unit of area in comparison with the outer surface. I found the relation to be as 8:5 in favor of the inner side. This is contrary to what we should expect, for in the foliage leaves of *Cyrtanthus* the stomata are more numerous on the abaxial surface.

Some of the ovules which were killed in the early stages were examined and found to contain an embryo sac of the lily type. The

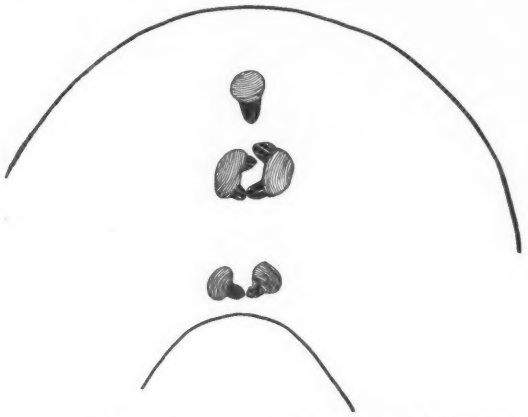


FIG. 2.—The vascular arrangement at the midrib of the carpel

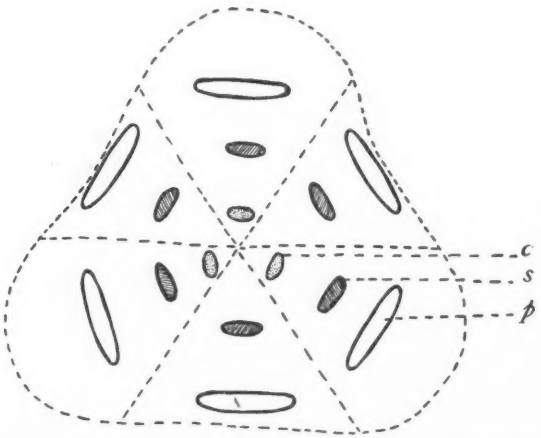


FIG. 3.—Diagram of a flower of *Cyrtanthus* against the ovary (dotted line), showing the relation between the vascular conditions and the parts of the flower; *p*, petals; *s*, sepals; *c*, carpels.

antipodals, synergids, and egg showed no departures from this type in the mature stage of the gametophyte; the development up to this stage was not seen.

Embryo

The literature of the embryos of monocotyledons is extensive but not satisfactory. The "sheath" was recognized, of course, early in the history of the study, and was presumed to be a single cotyledon, giving the name to the whole class. Besides the presence of the single cotyledon, early investigators were so impressed with the large amount of endosperm or "albumen," as they called it, occurring outside the embryos in such seeds, that they also called them "albuminous." As to the origin and nature of the cotyledonary sheath, various opinions are expressed, which fact perhaps demonstrates that there are various modes of origin. The earliest writers, HANSTEIN (3) and FAMINTZIN (4), described the embryo of *Alisma Plantago*, in which the cotyledon is terminal in origin. HEGELMAIER (5) describes it in some cases as arising from a cell near the tip, and being pushed into the terminal position by later development. SHAFFNER (6) says that in *Sagittaria* the cotyledon arises from the terminal cell of the proembryo. CAMPBELL (7) finds the same condition in *Naias;* the same author in his study of *Lilaea* (8) says that the sheath is not at first an enveloping organ, but that it becomes such by the lateral growth of its margins; and the same facts are repeated for the Araceae (9). WITTMACK (10) in his monograph on the Bromeliaceae has a drawing of a longitudinal section of the embryo of *Guzmannia tricolor*, taken through the center in such a way as to show the elongated side of the sheath on one side and the shorter side on the other. He calls the long side the "scutellum" and the short side the "cotyledon." There is nothing in his figure to show that scutellum and cotyledon are not one and the same structure, and yet it would seem that so reliable an investigator must have had some reason for applying the two terms in this way. BILLINGS (11) says that the cotyledon is terminal in origin, that the middle segment of the three-celled proembryo gives rise to all the other organs, and that before the stem tip is differentiated, the cells surrounding the area where it is to arise grow up into a ridge of tissue, which in the mature embryo incloses the growing point completely. Here the author seems to imply (1) that the sheath does not completely inclose the growing point in its inception, and (2) that the sheath is not the cotyledon, in the latter respect agreeing with WITTMACK.

A new impulse was given to the study of embryology when COULTER and CHAMBERLAIN began the revision of their *Morphology of gymnosperms* (15). Especially was the impulse felt among the cycads. Cycads were collected from the oriental and occidental tropics, and all phases of their life history investigated. The dicotyledonous nature of the cycadean embryo was demonstrated for all of them, even that of *Ceratozamia* (12, 13), which had been reported as having a single cotyledon. But while these embryos were shown to be normally dicotyledonous, exceptions to dicotyledony were seen to be by no means rare. The case of *Ceratozamia* was proved to be the result of abortion; but in *Microcycas* a condition was found in which the cotyledons were fused to such an extent that the author of the investigation referred to the fused structure as a "sheath," and expressed the suspicion that monocotyledony, even in angiosperms, might have arisen in both these ways: suppression, as in *Ceratozamia*, and fusion, as in *Microcycas*. COULTER and CHAMBERLAIN, in their chapter on evolutionary tendencies (15), seem to give credence to this suspicion by requesting Sister HELEN ANGELA to illustrate her views on the subject of the primitiveness of polycotyledony and the tendency to reduce the number of cotyledons.

From the material at my disposal, I was able to procure embryos in two different stages of development. The younger one was found to consist of an enveloping sheath, still meristematic and with four distinct lobes at its apex. Each lobe has its own vascular strand, four separate strands arising from the four poles of the root. The lobes are approximately equal in size at this stage, but not absolutely so, as can be seen from fig. 2. At the base of the sheath is the region from which the stem tip will arise later; at this stage it is not meristematic. Figs. 1 and 2 of the plate are sketches of the exterior and interior of the embryo at this stage, and fig. 3 is a cross-section which illustrates the irregular growth in thickness of the sheath, the region which bears the vascular strands resisting the pressure from without and giving the appearance of lobes and a four-sided aperture.

The second embryo studied (fig. 4) is older than the one just described. The sheath now consists of two regions, a lower portion

which still envelops the growing point, and a long upper projection which has resulted from the greater growth in length of one side of the sheath. The tip of the shorter, aborted side of the sheath is seen at *a* in figs. 4, 5, and 15. The vacant space in this older embryo, unlike that of the younger, which was four-lobed, is now reduced to the narrow slit represented by *s* in figs. 13 and 14. The vascular conditions are indicated in fig. 5. In the lower region of the sheath (the completely enveloping region below the abortion) each side has two vascular strands, making four in all (figs. 8–13), which arise independently from the cotyledonary node and enter the two differentiated sides of the sheath, just as happens in many dicotyledonous seedlings (figs. 5 and 7). Near the tip of the lower or aborted side of the sheath, the vascular strands from that side abruptly enter the region of the extended side, and fuse with the vascular strands of that organ.

At this stage of development, the growing point has differentiated the first and second leaves, the first arising on the side corresponding to the aborted side of the sheath, and the second one about opposite the first. All are closely pressed upon by the growing sides of the sheath. These arrangements are shown in figs. 5 and 10. The root cylinder is tetrarch (fig. 6).

Discussion

As was remarked before, the amount of endosperm in the seeds of *Cyrtanthus* is very great in proportion to the size of the embryo. This makes it difficult for the embryo to develop its organs to their full extent. I have noted how the originally large space within the sides of the sheath is reduced, little by little, as growth progresses, to a very small space (*s*, figs. 3, 13, and 14). Following out this process in thought, it is not difficult to imagine how the early condition indicated in fig. 3 might easily be changed into that of figs. 4 and 5 merely by the mechanical pressure of the large endosperm. In other words, the sheath of monocotyledons is probably a fusion of two or more cotyledons; the probability amounting almost to a certainty when we remember that the very same condition here described in a monocotyledon has been discovered in the dicotyledonous embryo of *Microcycas*, a complete fusion of the

two cotyledons. Looking at fig. 1 of pl. V in the *Microcycas* paper (14), and comparing it with my fig. 13, one would be puzzled to say which is the dicotyledon and which the monocotyledon. The same difficulty would arise by comparing my fig. 10 with fig. 13 of pl. VI of the *Microcycas* paper. Sister HELEN ANGELA was so impressed with the complete fusion of the two cotyledons that she called the fused structure a sheath.

Furthermore, a consideration of the vascular connections, the four root poles with their extensions finding full outlet in the sheath, shows that this sheath represents the whole cotyledonary apparatus, which, historically, finds its expression in many cotyledons in *Pinus*, in two in the normal cycads and dicotyledonous angiosperms, and in the sheath of monocotyledons.

This condition seems to me almost the last proof necessary to demonstrate the origin of monocotyledons from dicotyledons.

Summary

1. The embryo sac of *Cyrtanthus* seems to follow the regular *Lilium* type. The endosperm is very extensive.

2. Stomata are more numerous on the inner than on the outer surface of the carpel.

3. There are three separate bundles at the midrib of each carpel and two at the fusion of the carpels. This arrangement is related to the various parts of the flower.

4. The youngest observed stages of the embryo have the stem tip enveloped by a sheath with four lobes at its top.

5. In an older embryo the sheath is differentiated into a longer and a shorter side, the appearance and vascular anatomy of which give the distinct impression of two cotyledons.

6. Any pressure or fusion is referred to the extraordinary amount of endosperm.

7. The investigation is considered a last proof of the theory of monocotyledony from dicotyledony.

The author wishes to express her grateful acknowledgment to Dr. CHARLES J. CHAMBERLAIN for material, to Dr. JOHN M.

COULTER and Dr. W. J. G. LAND for kind assistance during the early part of the investigation, and to Sister HELEN ANGELA under whose direction it was completed.

THE COLLEGE OF SAINT ELIZABETH
CONVENT STATION, N.J.

LITERATURE CITED

1. Botanical Magazine, pl. 5218.
2. PAX, F., Monograph on Amaryllidaceae in ENGLER and PRANTL'S Natürlichen Pflanzenfamilien. 1889.
3. HANSTEIN, J., Entwickelungsgeschichte der Keime der Monocotyledonen und Dicotyledonen. Bot. Abhandl. Bonn. p. 112. 1870.
4. FAMINTZIN, A., Embryologische Studien. Mém. Acad. Imp. Sci. St. Pétersbourg **26**:10. 1879.
5. HEGELMAIER, F., Zur Entwickelungsgeschichte monocotyledoner Keime nebst Bemerkungen über die Bildung der Samendeckel. Bot. Zeit. **32**: 631. 1874.
6. SHAFFNER, J. H., Contribution to the life history of *Sagittaria variabilis*. BOT. GAZ. **23**:252–273. 1897.
7. CAMPBELL, D. H., A morphological study of *Naias* and *Zannichellia*. Proc. Calif. Acad. Sci. III. 1:1–62. 1897.
8. ———, The development of the flower and embryo in *Lilaea subulata* HBK. Ann. Botany **12**:1–28. 1898.
9. ———, Studies on the Araceae. Ann. Botany **14**:1–25. 1900.
10. WITTMACK, L., Monograph on Bromeliaceae in ENGLER and PRANTL'S Natürlichen Pflanzenfamilien. 1889.
11. BILLINGS, F. H., A study of *Tillandsia usneoides*. BOT. GAZ. **38**:99–121. 1904.
12. ANGELA, Sister HELEN, The embryo of *Ceratozamia:* a physiological study. BOT. GAZ. **45**:412. 1908.
13. ———, The seedling of *Ceratozamia*. BOT. GAZ. **46**:205. 1908.
14. ———, Vascular anatomy of the seedling of *Microcycas calocoma*. BOT. GAZ. **47**:139–147. 1909.
15. COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of gymnosperms. Chicago. 1910.

EXPLANATION OF PLATE XXIV

The drawings were made with the aid of an Abbé camera lucida, the magnification used being 120 diameters. In every case, *a* indicates the tip of the aborted or short side of the sheath, *c* the longer side, and *s* the space within the sheath.

FIG. 1.—Exterior view of a young embryo before the differentiation of the two portions of the sheath.

FIG. 2.—Longitudinal section through the center of the embryo shown in fig. 1.

FIG. 3.—Cross-section of a young sheath above the region of the growing point of the stem.

FIG. 4.—Exterior view of an older embryo, showing differentiation of both sides of the sheath.

FIG. 5.—Longitudinal section (partly reconstructed and diagrammatic), showing the first leaf, the growing point, and the behavior of the vascular bundles.

FIG. 6.—Cross-section through the root cylinder of the older embryo.

FIG. 7.—Cross-section of the cotyledonary node, showing the independent origin of the four bundles.

FIG. 8.—Cross-section just above the cotyledonary plate; the four bundles have assumed the vertical position.

FIG. 9.—Cross-section above that represented in fig. 8, showing the stem cylinder.

FIG. 10.—Section above the preceding, showing the first leaf and the growing point.

FIG. 11.—Cross-section above the tip of the second leaf.

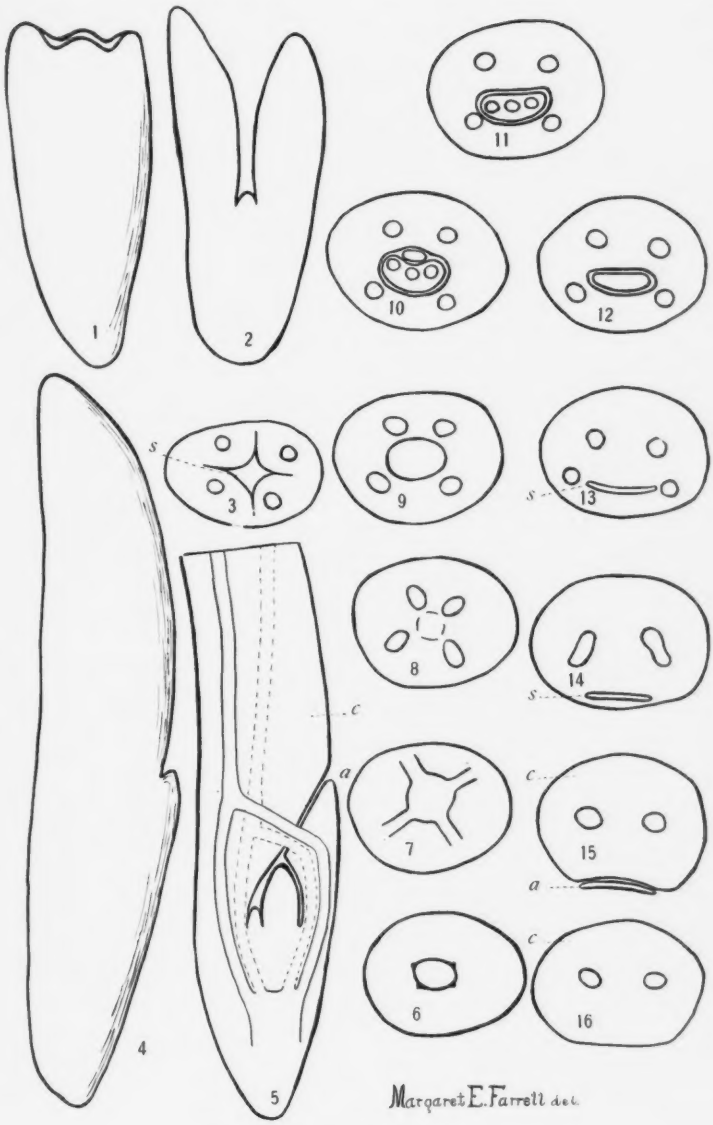
FIG. 12.—Cross-section just above that shown in fig. 11; it shows the tip of the first leaf.

FIG. 13.—Cross-section above the tip of the first leaf; shows the space or slit between the two sides of the sheath.

FIG. 14.—A section showing the fusion of the four bundles to make two; it was made immediately above that shown in fig. 13.

FIG. 15.—A section near the tip of the aborted side of the sheath, giving the appearance of two cotyledons lying side by side.

FIG. 16.—A cross-section in the upper part of the sheath.



FARRELL on CYRTANTHUS

CURRENT LITERATURE

BOOK REVIEWS

Textile fibers

A book by STIRM[1] on the chemical technology of textile fibers deals with every phase of the derivation and handling of the fibers: source, method of obtaining, physical and chemical character, washing and bleaching of the raw fiber, preparation for stamping and dyeing, and stamping and dyeing themselves. The work covers plant fibers (cotton and various bast fibers, such as flax, hemp, jute, and manila), animal fibers (wool, hair, and silk), mineral fibers (asbestos), and artificially produced fibers from mineral raw materials (glass and mineral fiber) and from plant raw materials (India rubber fiber and artificial silk). The work on plant fibers reminds the botanist of the detail with which these technical workers have studied the histology, chemistry, and physics of cotton, bast, etc. In the case of cotton, one finds a good summary of our knowledge of the histology and microchemistry of the fiber. The chemical composition of the fiber is given, including the substances involved as impurities, with methods of removal. The chemistry of cellulose is dealt with briefly, with various theories as to its molecular weight and structural formula. The behavior of cellulose toward many reagents in various concentrations (acids, bases, salts, oxidizing and hydrolizing agents, and various solvents) is clearly summarized. The changes involved in such processes as bleaching, mercerization, and formation of artificial silk are discussed, along with the theories offered in explanation. The author recognizes many of the problems with cellulose as belonging to the field of colloidal chemistry. The histology and chemistry of bast fibers receive like consideration. The work reminds one that the knowledge useful to the technical worker is often the same as that which is of significance to the "pure" scientist.—WILLIAM CROCKER.

MINOR NOTICES

The Journal of Ecology.—It is rare that a new journal starts off so well as does the *Journal of Ecology*,[2] the first volume of which is now completed. In 1904 a great advance was made in ecological study in the British Isles by the

[1] STIRM, KARL, Chemische Technologie der Gespinnstfasern. xvi+410. Berlin: Gebrüder Borntraeger. 1913.

[2] The Journal of Ecology, edited for the British Ecological Society by FRANK CAVERS. Cambridge University Press (American agent: The University of Chicago Press). Volume I. 1913. Price per annum, $3.75.

organization of the Central Committee for the Survey and Study of British Vegetation, more popularly known as the British Vegetation Committee. This organization secured the effective cooperation of British ecologists, and among other things has to its credit the organization of the International Phytogeographic Excursion of 1911 and the publication of *Types of British vegetation*. In 1912 there was formally organized the British Ecological Society, which has become the successor of the British Vegetation Committee. One of the chief tasks of this new society is the publication of a journal. The first thought was to have this new journal be little more than an organ of the British ecologists. But a broader view prevailed, and we now have an international journal devoted to ecology, the first of its kind; from the first number the quality of the journal has been such as to give it rank with the foremost botanical periodicals.

The scope of the new ecological journal is such as to make an effective appeal to ecologists of other lands quite as much as to those of the British Isles. To facilitate use by both general and local readers, articles and reviews of general nature are kept distinct from those of more local significance. To the writer the "high-water mark" of the new journal seems to be reached by its reviews. It is doubtful if the reviews in any other botanical journal equal in efficiency those of the new *Journal of Ecology*. They are models as to thoroughness and accuracy, in many cases making it really unnecessary to consult the original papers except to secure details. It is unusual and highly illuminating to have published in many of the reviews the more significant illustrations of the original papers. The only adverse criticism that the writer would make is that the reviews generally are unsigned. It goes without saying that the new journal is absolutely necessary for the working ecologist. The British ecologists may well congratulate themselves upon their accomplishments during the last decade. In 1904 their work was scattered and mostly of local significance; today they are unquestionably the leaders in cooperative ecological activity.—H. C. COWLES.

American Journal of Botany.—The first number of this new journal has appeared, and needs no explanation to American botanists. It is the official publication of the Botanical Society of America, and is published by the Brooklyn Botanic Garden. The introductory statement by the editor-in-chief, Professor F. C. NEWCOMBE of the University of Michigan, shows that the increase of means of publication has not kept pace with production. "The result has been that our established botanical journals in America are overstocked with manuscripts waiting their turn, our colleges and universities are making outlets for their own production, and foreign journals have their courtesy and capacity taxed by the offers of American contributors. All three of the conditions just named are undesirable: an author does not like to wait a year or more for the publication of his paper, the multiplication of small periodicals by colleges and universities is a vexation to research, and it is neither

just to ourselves nor kind to our colleagues of other lands to ask them to give large printing space to our contributions." It is evident that the new journal will relieve this pressure somewhat, which the established journals have felt keenly.

This initial number contains the following papers: "The development of *Agaricus arvensis* and *A. comtulus*," by GEO. F. ATKINSON; "Studies of teratological phenomena in their relation to evolution and the problems of heredity. I," by ORLAND E. WHITE; "Nuclear behavior in the promycelia of *Caeoma nitens* Burrill and *Puccinia Peckiana* Howe," by L. O. KUNKEL; and "An axial abscission of *Impatiens Sultani* as the result of traumatic stimuli," by R. A. GORTNER and J. A. HARRIS.—J. M. C.

Illinois Academy of Science.—The volume of *Transactions* of the Illinois Academy of Science for 1913 contains the following botanical papers: "Annotated list of the algae of eastern Illinois," by E. N. TRANSEAU; "Reproduction by layering in the black spruce," by GEO. D. FULLER; "Evaporation and soil moisture on the prairies of Illinois," by E. M. HARVEY; and "The stratification of atmospheric humidity in the forest," by GEO. D. FULLER, J. R. LOCKE, and WADE MCNUTT.—J. M. C.

NOTES FOR STUDENTS

Paleobotanical notes.—ARBER[3] has done a most useful service in revising the seed-impressions of the British Coal Measures, and putting them into more definite categories. The most recent list, that of KIDSTON in 1894, included 5 genera with 19 species. ARBER'S revision contains 14 genera with 37 species. These detached seed-impressions belong to both Cycadofilicales and Cordaitales, whose seeds cannot be distinguished. Of the 14 genera recognized 9 are new (*Platyspermum*, *Cornucarpus*, *Samarospermum*, *Microspermum*, *Megalospermum*, *Radiospermum*, *Neurospermum*, *Schizospermum*, *Pterospermum*). In addition to the diagnosis of genera and species, every British species is figured.

Mrs. ARBER[4] has examined sections of a new specimen of *Trigonocarpus*, showing that the sclerenchyma of the micropylar beak is preserved as far as its extreme apex, and also that the nucellus was free from the integument almost to the base of the seed.

KNOWLTON[5] has described a collection of Jurassic plants from Alaska, obtained between latitudes 68° and 69°. SEWARD'S report on a collection of

[3] ARBER, E. A. NEWELL, A revision of the seed-impressions of the British Coal Measures. Ann. Botany **28**:81–108. *figs. 8. pls. 6–8.* 1914.

[4] ARBER, AGNES, A note on *Trigonocarpus*. Ann. Botany **28**:195, 196. *fig. 1.* 1914.

[5] KNOWLTON, F. H., The Jurassic flora of Cape Lisburne, Alaska. U.S. Geol. Survey. Professional paper 85-D. pp. 39–55. *pls. 5–8.* 1914.

Jurassic plants from Siberia (Amurland) makes a comparison of Alaskan and Siberian Jurassic floras possible. KNOWLTON concludes that the striking similarity between the Jurassic floras of northwestern North America and eastern Siberia shows that the land connection between these regions during the Jurassic must have been practically continuous. The Alaskan list recognizes 12 genera and 17 species, the solitary species of *Equisetum* being described as new. The dominance of cycadophytes is obvious, so far as it can be inferred from so small a number of species, the list being as follows: pteridophytes 5; cycadophytes 11; and *Ginkgo* represented by a single species.

SALISBURY[6] has described in detail a new species of *Trigonocarpus* obtained from the Lower Coal Measures at Shore Littleborough, England. In addition to the well marked features of the sclerotesta and sarcotesta, the nucellus is almost completely free from the integument, and has a well developed and thick walled epidermal layer, three longitudinal flanges corresponding with the commissures, and numerous secretory sacs in the ground tissue. The conclusion is reached that this species is more primitive than its congeners, and that the testa arose from the lateral fusion of a whorl of six originally free members. A discussion of the resemblances and differences between the Trigonocarpeae and the Lagenostomales reaches the conclusion that they are to be explained by intercalated growth, followed by subsequent fusion of the nucellus and integument.

Dr. STOPES[7] has published a very interesting lecture upon the past and future of paleobotany, delivered at University College, London. The thesis is that paleobotany is now an independent science, contributing to both botany and geology, and with its own important field.

THOMAS and BANCROFT[8] have made a detailed comparative study of the cuticle of recent and fossil cycads, including also mention of other gymnosperms, especially with reference to the form and structure of the stomata. The general conclusion is that the characters presented by the stomata and epidermal cells of gymnosperms are important as indicating to some extent their relationships. Among the cycadophytes there are some characters which have undergone little modification from the Jurassic to the present time, and the authors conclude that stomatal structure is the expression of ancestral characters rather than of purely local and temporary conditions of environment.—J. M. C.

---

[6] SALISBURY, E. J., On the structure and relationships of *Trigonocarpus shorensis*, sp. nov. A new seed from the Paleozoic rocks. Ann. Botany **28**:39–80. *figs. 8. pls. 4, 5.* 1914.

[7] STOPES, MARIE C., Paleobotany; its past and its future. Knowledge **37**: 15–24. 1914.

[8] THOMAS, H. HAMSHAW, and BANCROFT, NELLIE, On the cuticles of some recent and fossil cycadean fronds. Trans. Linn. Soc. London II. Bot. **8**:155–204. *figs. 32. pls. 17–20.* 1913.

Hydrogen and alcoholic fermentation.—Through a study of the reduction of methylene blue, in the presence of yeast, LVOFF[9] has found further evidence that reductase plays an essential rôle in alcoholic fermentation. Methylene blue is rapidly decolorized when placed in a yeast culture. This decoloration is brought about through the absorption of two atoms of nascent hydrogen (molecular H is not effective) at the double bond of the color group. Reductase activates the hydrogen. He finds the output of alcohol and CO_2 greatly lowered while the methylene blue is being reduced. Therefore the hydrogen, activated by the reductase, probably goes directly to the methylene blue molecule, thereby arresting the further normal steps of the fermentation process. Quantitative determinations of the CO_2 and alcohol produced and the hydrogen absorbed (by the methylene blue) showed that one gram-molecule of methylene blue takes from the fermentation medium one gram-molecule of hydrogen and "inactivates" one gram-molecule of hexose, thus preventing the splitting into alcohol and CO_2. Unfortunately, a study of this "inactivated" carbohydrate molecule has not been made.

Again, yeast when mixed with water only still has the capacity for reducing methylene blue. CO_2 is given off at the same time in amount directly related to the methylene blue reduced; for example, one gram-molecule methylene blue, under conditions favoring self-fermentation, takes one gram-molecule of hydrogen from the medium, liberating one gram-molecule of CO_2. The source of this CO_2 is yet unexplained. However, the author suggests the possibility that it comes from the fermentation of amino acids in the yeast, a suggestion in agreement with the work of EHRLICH, and particularly with that of BACH, where from amino acids in the presence of alloxan, NH_3, CO_2, and 2H are eliminated (the 2H passing to the alloxan), leaving an aldehyde in the medium. —E. M. HARVEY.

Cytology and embryology of Smilacina.—*Smilacina* was studied some time ago by LAWSON,[10] who reported that synapsis is due not to a marked contraction of the nuclear contents, but to a sudden enlargement of the nuclear cavity, which gives the appearance of a contraction. MCALLISTER[11] claims that synapsis is due to contraction and not to any considerable enlargement of the nuclear cavity. It would seem as if this should be settled by measurement rather than by discussion, but since both men studied *Smilacina* and both made measurements, an extensive series of measurements of various forms would seem to be in order.

---

[9] LVOFF, GERGIUS, Hefegärung und Wasserstoff. Zeitschr. Gärungsphysiol. **3**: 289–320. 1914.

[10] LAWSON, A. A., The phase of the nucleus known as synapsis. Trans. Roy. Soc. Edinburgh **47**:591–604. *pls. 2*. 1911. Rev. in BOT. GAZ. **51**:313. 1911.

[11] MCALLISTER, F., On the cytology and embryology of *Smilacina racemosa*. Trans. Wis. Acad. Sci. **17**:599–660. *pls. 56–58*. 1913.

During synapsis McALLISTER finds that there is a lateral pairing and fusion of spirems, the fusion being complete at the time of the recovery from synapsis. After this recovery there is a second contraction stage. The double heterotypic chromosomes are formed, not by the approximation of the limbs of loops, but by a transverse segmentation of a longitudinally split spirem, the line of the split probably representing the line of approximation of the two parental spirems seen at synapsis.

The heterotypic and homotypic mitoses in the megaspore mother cell result in the formation of four megaspores, separated by plasma membranes. The membrane formed at the heterotypic mitosis persists, while those formed at the homotypic mitosis quickly break down. From the inner binucleate cell, thus formed, an 8-nucleate embryo sac is developed. Consequently, two megaspores are concerned in the development of the embryo sac.

Adventitious embryos develop from nucellar cells in the micropylar region, and one or more of them may become mature. The presence of pollen tubes indicates that embryos may also result from fertilization.—CHARLES J. CHAMBERLAIN.

Marine algae.—BORGESEN[12] has published an account of the marine Chlorophyceae of the Danish West Indies, based upon collections made in 1892, 1895, and 1905. The list contains 34 genera including 86 species, 4 new species being described in *Cladophora* (2), *Avrainvillea*, and *Pringsheimia*. The full field notes and the numerous illustrations make the account an exceedingly satisfactory one.

BORGENSEN[13] has also given an account of the species of *Sargassum* collected during his three visits to the Danish West Indies, partly along the coasts of the islands, and partly in the Sargasso Sea. The shore collections include 4 species, while the pelagic collections are all referred to two species. The discussion of the "biology, affinities, and origin of the gulfweed" is especially interesting. The conclusions reached are that the gulfweed of the Sargasso Sea consists of two species, *S. natans* (most common) and *S. Hystrix*, var. *fluitans;* that they are true pelagic algae, living perennially on the open sea; and that most probably they have descended from shore forms of the West Indies and the neighboring American coast. The author says "it is of great interest that we have an instance of floating, pelagic species of such a high alga type as *Sargassum;* because, as is well known, the higher types of algae are as a rule attached, and if detached they perish sooner or later."—J. M. C.

---

[12] BORGENSEN, F., The marine algae of the Danish West Indies. Part I. Chlorophyceae. Dansk Botanisk Arkiv 1: no. 4. pp. 158. *figs. 126* and *chart.* 1913. Copenhagen: H. Hagerup. *Kr* 4.

[13] ———, The species of *Sargassum* found along the coasts of the Danish West Indies, with remarks upon the floating forms of the Sargasso Sea. Mindeskrift for Japetus Steenstrup. pp. 20. *figs. 8.* 1914.

Reproduction in Scenedesmus.—Although *Scenedesmus* is a very familiar alga, the details of its reproduction had not been investigated, doubtless because the cells are so small. SMITH[14] has studied the cell structure and reproduction in all of the three species. The cells are strictly uninucleate, contain a single pyrenoid, and have a cell wall consisting of two layers. When 4-celled colonies are formed, the steps are as follows: The first nuclear division is followed by a transverse cleavage of the cytoplasm, and nuclear division in the two resulting protoplasts is followed by cleavage furrows at right angles to the first furrow. The pyrenoid then disappears and the uninucleate protoplasts elongate until they extend the entire length of the mother cell. A pyrenoid is now formed *de novo* within each of the four cells, and cell walls appear. The young colony escapes through a longitudinal rupture in the wall of the mother cell and assumes the characteristic arrangement by unrolling. In the formation of 8-celled colonies, there are three nuclear divisions, the second and third being followed by cytoplasmic cleavages. The material for the study was grown in pure cultures. Sections were cut from 3–5 μ in thickness and stained in Flemming's safranin-gentian violet-orange combination.—C. J. CHAMBERLAIN.

The embryo of Gyrostachys.—The origin and development of the embryo sac of *Gyrostachys*, more commonly known as *Spiranthes*, is described for two species, *S. gracilis* and *S. cernua*, by Miss PACE,[15] whose previous work allows her to speak with authority upon this subject. The embryo sac is very irregular in its development, sometimes arising from 4 megaspores, sometimes from 2, and sometimes from only one. At the fertilization stage the embryo sac may contain 4, 5, 6, or 8 nuclei, the 6-nucleate condition, resulting from a lack of one mitosis in the chalazal end of the sac, being the most frequent. The diploid number of chromosomes in *S. gracilis* is 30, and in *S. cernua* 60; consequently, the relation, in this respect, is similar to that between *Oenothera Lamarckiana* and *O. gigas*, and *S. cernua* might be called a tetraploid form. As is well known, *S. cernua* is a larger and more vigorous species, and the gigantism is evident also in the size of the ovary, the ovules, and the size of the cells. Miss PACE suggests that the subject might be worth investigating experimentally.—CHARLES J. CHAMBERLAIN.

Westphalian Calamariaceae.—A revision of the European Calamariaceae, undertaken in conjunction with KIDSTON, impressed upon JONGMANS the fragmentary condition of our knowledge of the Calamariceae of the Rheinish-Westphalian coal fields, and also the inadequacy of the descriptions and figures. Accordingly, with the cooperation of KUKUK,[16] he examined and described

[14] SMITH, GILBERT M., The cell structure and colony formation in *Scenedesmus*. Archiv für Protistenkunde **32**:278–297. *pls. 16, 17.* 1914.

[15] PACE, LULA, Two species of *Gyrostachys*. Baylor University Bull. **17**:1–16. *pl. 1.* 1914.

[16] JONGMANS, W. J., and KUKUK, P., Die Calamariaceen des Rheinisch-Westfälischen Kohlenbeckens. Mededeelingen van's Rikjs Herbarium. Leiden. no. 20. Text 8vo. pp. 89. Atlas 4to. *pls. 22.* 1913.

specimens from the following collections: K. Pr. Geol. Landesanstalt, Berlin; Städt. Museum, Chemnitz; Naturw. Museum, Dortmund; K. K. Geol. Reichsanstalt, Wien; Märkisches Museum, Witten; Museum, Osnabrück; s'Rijks Herbarium, Leiden; Geol. Institut der Universität, Göttingen; Geol. Institut der Bergakademie, Clausthal; and Geol. Institut der Universität, Münster i.W.

The work is strictly taxonomic. The descriptions and synonomy are very complete, and the magnificent plates enable one to study the subject almost as well as if he had the actual specimens in his hands.—CHARLES J. CHAMBERLAIN.

Anatomy of petioles of Cycads.—LE GOC[17] has studied the debated xylem situation in the foliar bundles of the cycads. As is well known, both centripetal and centrifugal xylem occur, a situation which has been variously interpreted, but in general the bundle has been spoken of as mesarch. LE GOC has found that at the very base of the petioles in cycads the xylem is entirely centrifugal, and that later the bundles assume different forms, becoming concentric, collateral, or a combination of these two arrangements. He regards the centrifugal xylem at the base as a secondary growth, and the centripetal xylem which appears later as a primary structure, laid down early, but only gradually lignified. The two xylems he thinks are probably distinct in origin, appearing in response to "physiological demands but morphologically discontinuous." During most of the course of the bundles along the petiole the two xylems remain distinct, and therefore he would suggest that the bundle is more properly called "pseudo-mesarch."—J. M. C.

The origin of the "eye spot."—From a study of the literature, without any apparent study of the structures themselves, ROTHERT[18] comes to the conclusion that the "eye spot" of flagellates and algae is derived from a plastid. The evidence seemed clear already, so far as the Euglenaceae are concerned, and GUIGNARD, as long ago as 1889, claimed that the "eye spot" seen in the sperms of *Fucus* arose from a colorless plastid. ROTHERT overlooks entirely the various papers by YAMANOUCHI from 1909 to 1913, particularly the paper on *Cutleria*,[19] in which the origin and development of the "eye spot" are described in detail.—C. J. CHAMBERLAIN.

---

[17] LE GOC, M. J., Observations on the centripetal and centrifugal xylems in the petioles of cycads. Ann. Botany **28**:183–193. *pl. 11. fig. 1.* 1914.

[18] ROTHERT, WLADISLAW, Der "Augenfleck" der Algen und Flagellaten ein Chromoplast. Ber Deutsch. Bot. Gesells. **32**:91–96. 1914.

[19] YAMANOUCHI, SHIGÉO, The life history of *Cutleria*. BOT. GAZ. **54**:441–502. *figs. 16. pls. 26–45.* 1912.